UTRECHT MICROPALEONTOLOGICAL BULLETINS

H. LAAGLAND

CYCLOCLYPEUS IN THE MEDITERRANEAN OLIGOCENE

39

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ABSTRACT

Fossil assemblages have been studied of the larger foraminiferal genus *Cycloclypeus* of the family Nummulitidae. The specimens were collected from 28 Oligocene samples from Spain, Italy and Israel.

The external and internal morphologies of the tests were examined. In a number of samples a distinct and continuous variation is present from smooth specimens to specimens showing a well developed sculptural relief. Specimens of a restricted number of samples were grouped into classes according to the height of the ornamentation.

After sectioning of the specimens the internal morphology was examined. Several parameters were counted and measured, including two parameters for the size of the embryonic chambers, one for the number of preyclic chambers, one for the number of spiral convolutions and one for the maximum diameter of the precyclic stage. In one sample the ontogenetic development of specimens was studied by measuring a number of parameters in successive precyclic chambers. The morphometrical data on internal morphology were treated statistically.

Data show that in the Mediterranean region the stratigraphic range of *Cycloclypeus* comprises the entire Upper Oligocene (P21/N2 - P22/N3; NP24 - NP25), possibly extending downwards into the uppermost part of the Lower Oligocene. In the lower and middle parts of its range the genus is represented by the species of the *droogeri*-lineage, in wich the number of the precyclic chambers is reduced from an assemblage average of about 30 to one of about 16. In the upper part of the Upper Oligocene the representatives of this lineage were replaced by the immigrant species *Cycloclypeus eidae*. The assemblages of this species are very similar to those reported from the Indo-Pacific province and in one sample even the mixing of two types of megalospheres was recorded, which is typical of the Indo-Pacific occurrences. In the Mediterranean region the genus probably became extinct at the very end of the Oligocene.

Data indicate that nepionic evolution in *Cycloclypeus* primarily concerns the reduction in the size of the precyclic stage. This resulted in the reduction of the number of nepionic chambers, representing the number of growth-steps necessary to reach this nepionic size.

In data on internal and external morphology there is no evidence for the existence of two separate contemporaneous lineages in the Mediterranean Oligocene, which would differ in external morphology. Differences in ornamentation of specimens are ascribed to differences in the depth at which specimens lived before their remains were washed together and transported

down to the depth of deposition. By their glassy pustules specimens living at greater depth probably made more efficient use of of the restricted light-intensities, enabling the photosynthetic activity of the symbionts living within their tests.

In a number of samples it has been checked whether groups of specimens differing in ornamentation and therefore in average depth of habitat, also differ in internal morphology. The results are compared with data on recorded and alleged depth-clines in other groups of living and fossil larger foraminifera, which data are critically reviewed.

It is concluded that in the *droogeri*-lineage a depth-cline in embryon-size was present. It basically consisted of a modest size-increase with increasing depth of habitat, which is thought to have been related to waning light-intensities. Locally or regionally, however, elevated levels of productivity may have induced an increase in average embryon-size in some middle part of the depth range, which was superimposed on the trend of sustained increase with depth.

In the Cycloclypei from Israel clinal variation in the number of precyclic chambers is mainly ascribed to the depth-related variation in embryon-size. In European *Cycloclypeus* a reduction in the number of precyclic chambers is apparent with increasing depth of habitat. This is ascribed to the concurrent reduction in the size of the precyclic stage.

Relations between clinal variation and evolutionary development in embryon-size and in nepionic configuration are discussed. Evolution and clinal variation are interpreted in terms of light-intensity, growth-activity and life-strategy. It is suggested that clinal variation acted as a driving force in the process of nepionic evolution in European *Cycloclypeus*.

Chapter I

INTRODUCTION

I.1 GENERAL CONCEPTS

This monograph deals with representatives of the genus *Cycloclypeus* of the family Nummulitidae, which lived in the Mediterranean realm during Oligocene times. Like the related and well-known genus *Nummulites* the genus *Cycloclypeus* belongs to the informal and heterogeneous group of the so-called larger foraminifera. These unicellular organisms, commonly ranging in size from about half a milimetre to several centimetres, live and have lived on the bottom of the shallow parts of tropical and subtropical seas. These organisms build a shell which in *Cycloclypeus* is composed of calcareous material and which grows as new chambers are being added. After the death of the organism this so-called test may become buried in the sediment.

Larger foraminifera have been the subject of detailed paleontological studies. Various evolutionary trends in the size and shape of parts of the test have been recognized in a large number of groups. These trends are studied best by measuring and counting the relevant morphological features. Usually the test has to be prepared in some way to expose the particular parts to be studied.

As normally some natural variation in the studied trait is present in specimens from a single sample, data are gathered from a restricted number of randomly selected tests, which is thought to represent the total assemblage of specimens in the sample sufficiently well. From these numerical results mean values and other statistics are calculated. This allows for determination of the assemblage in the sample because biometric species have been defined by setting minimum and maximum values to these means.

Another important topic in the study of larger foraminifera concerns the observed and presumed relation between the morphology of the shell and environmental factors, such as depth of habitat, hydrodynamic energy and light-intensity. Such morphological trends along environmental gradients are called (morpho-)clines. In larger foraminifera changes related to depth of habitat are observed in the external as well as internal morphology of the test. Such changes occur for instance in the shape and ornamentation of the test but also in the size of the initial chambers. Also in the study of clinal variation morphometrical methods are applied.

I.2.1 The genus Cycloclypeus

The genus *Cycloclypeus* was established by Carpenter in 1856 on recent specimens dredged 'from a considerable depth of water off the coast of Borneo'. The disc-shaped tests are several milimetres to centimetres in diameter. The larger part is built of concentric chambers which are subdivided by septula into chamberlets (plates 6-9).

Carpenter already mentioned the presence of a canal-system in the walls of the chambers and chamberlets. This is a characteristic trait of all the representatives of the family Nummulitidae. It consists of a systematically arranged set of communicating cavities. The system shows openings into the chambers and chamberlets as well as openings to the ambient environment (plate 5, figs. 1-3). Hottinger (1977b) investigated the canal-system of *Cycloclypeus* by making use of refined preparation-methods and scanning-electron photographs. These canal-systems in Nummulitids are filled with protoplasm and enable the extrusion of pseudopods for purposes of locomotion and feeding.

In external appearance the test of recent *Cycloclypeus* may be smooth or ornamented by pustules. For the latter morphotypes the species-name *C. carpenteri* is available which is the type-species of the genus.

In the recent environment representatives of the genus occur in the deeper parts of the photic zone in the Indo-Pacific province. Here it lives on the bottom and its life-activities are probably supported to a considerable extent by the photosynthetic activity of algal symbionts. According to Silvestri (1896) the genus would also live in the Adriatic Sea. However, this interesting report was never corroborated by other records of *Cycloclypeus* in (sub-)recent waters or sediments of the Mediterranean realm.

From its origin in Oligocene time onward the genus has always been most abundant in the Indo-Pacific province. It is also present in Oligocene sediments in the Mediterranean region. Here, however, the genus is far less common. In this area it probably became extinct at the end of the Oligocene or soon after the beginning of the Miocene. In and around the Indian Ocean the fossil and recent record of *Cycloclypeus* is very poor. From the Atlantic and from the American province the genus has never been reported.

A homeomorph of the genus lives in the Red Sea and in the western part of the Indian Ocean. It is called *Heterocyclina tuberculata* and shows a large number of spirally arranged chambers preceding the later formed cyclical chambers. This build is also typical of primitive Oligocene *Cycloclypeus* and shows resemblance to the internal morphology of *Heterostegina*. The latter

genus also belongs to the Nummulitids but lacks the cyclical chambers present in *Cycloclypeus* and *Heterocyclina*. Instead, all its chambers are arranged in a spire.

Although primitive *Cycloclypeus* and recent *Heterocyclina* are very similar in internal and external appearance, they originate from different *Heterostegina*-ancestors and are therefore only distantly related. This is further corroborated by a systematic difference in the arrangement of the openings (stolons) which connect the chambers and chamberlets (Hottinger 1977a, 1977b).

I.2.2 The Indonesian Cycloclypei

Cycloclypeus was the first group of larger foraminifera which was studied morphometrically. Tan Sin Hok (1932) wrote a monograph on the Indonesian Cycloclypei. He sectioned a number of specimens from each of his samples and measured the diameter of the first chamber of the test, which is called the protoconch.

Occasional specimens showed a first chamber of distinctly smaller size ($\pm$ 25 μ) than the other specimens of the same sample. This kind of dimorphism is quite common in larger and smaller foraminifera. The specimens with small protoconchs are called microspheric or microspheres and the other specimens megalospheric of megalospheres. The two types of specimens represent different phases in the lifecycle of the species. The microspheric specimens result from the fusion of two gametes (sexual reproduction or gamogony). The megalospheric specimens are the result of asexual reproduction (schizogony).

In megalospheric Cycloclypei the globular protoconch is followed by a more or less kidney-shaped second chamber (plates 6-9). These first two chambers are different in shape from the subsequent crescent-shaped chambers. The early two chambers are called the embryonic chambers by Tan or simply the embryon.

The subsequent chambers are arranged in a spire. Usually starting with the fourth chamber, these so-called nepionic chambers become subdivided into chamberlets. In this suite of nepionic chambers chamber-length increases relative to the circumference of the preceding part of the test. As a result chambers become more and more strongly embracing up to the stage at which both chamber-ends meet and a cyclical or neanic chamber is formed. This marks the end of the nepionic stage and the beginning of the neanic stage in the life-history of single specimens.

Tan Sin Hok counted the number of nepionic chambers in his Cycloclypei. This parameter was later referred to as parameter X by Drooger (1955). For

each sample Tan calculated mean values of the protoconchal diameter in specimens with the same number of nepionic chambers. From these data (presented by Tan) mean parameter values can be calculated per sample for all the specimens Tan subjected to his counts and measurements.

Tan found that the number of nepionic chambers in his Cycloclypei decreased in the course of geologic time. In a later paper he called this evolutionary reduction of the number of spiral chambers nepionic acceleration. Similar evolutionary trends have since been found in other groups of larger foraminifera. In *Cycloclypeus* these trends lead to a reduction of the spirally arranged part of the test, in favour of the cyclical or radial chamber arrangement, which is introduced earlier in ontogeny. These trends are generally brought in connection with a passive mode of life of these larger foraminifera.

Tan's data on the number of nepionic chambers show a peculiar aspect. Variants with certain numbers of nepionic chambers are more frequent than other X-variants. These more frequent variants at fixed X-values Tan called elementary species. According to Tan evolution in *Cycloclypeus* had proceeded by the rise and fall of successive elementary species with decreasing numbers of nepionic chambers.

No such remarkable distribution patterns were found in subsequent studies by Cosijn (1938) on European *Cycloclypeus* and by Drooger (1955) in Indonesian samples. These and later authors ascribed Tan's results to subjective judgement in the often difficult process of assessing the exact number of nepionic chambers in the sections.

In his most primitive and oldest *Cycloclypeus* assemblage Tan recorded an average number of nepionic chambers of 28.8. Since MacGillavry's 1962 paper both the protoconch and deuteroconch are included in the X-count. Tan's *koolhoveni* assemblage therefore has an average X-value of 30.8.

In Tan's next younger assemblages mean X-values decrease from 26.7 to 23.8. For these assemblages Tan established the name of *Cycloclypeus oppenoorthi*. *C. koolhoveni* and *C. oppenoorthi* together constitute the *koolhoveni*-lineage. In view of the restricted range of mean values recorded in the assemblages of the *koolhoveni*-lineage we think that no more than one biometric species should be distinguished. Therefore *C. oppenoorthi* is regarded as a junior synonym of *C. koolhoveni*.

Tan's successive assemblages of the *koolhoveni*-lineage show an overall increase in the mean value of the protoconch-diameter of megalospheric specimens from about 150 μ to 180 μ. This kind of size-increase of embryonic chambers has also become well-known as a common evolutionary trend in larger foraminifera.

In Tan's next younger assemblages of Late Oligocene to Early Miocene age mean X-values have become further reduced, varying between 19 and 16. However, there is a marked reduction in the size of the embryonic chambers (mean protoconch-diameter values varying from about 80 to 120 μ) as well as in the size of the nepionic part of the test. For these assemblages Tan established the name of *C. eidae*. In the younger of these assemblages specimens with small protoconchs become accompanied by others with distinctly larger protoconchs and smaller numbers of chambers. Still younger samples clearly contain a mixture of both types of specimens. These more advanced mixtures Tan called *C. posteidae*. Similar mixed assemblages from Miocene deposits of Borneo were studied by Drooger (1955). The frequency-distributions of parameter X and of the protoconch-diameter (d) are clearly bimodal, showing dents at the values of X = 12 and d = 125 μ.

Eventually the Cycloclypei with small protoconchs are outnumbered and vanish from the record entirely. The remaining Cycloclypei with large protoconchs constitute again homogeneous assemblages. In subsequent assemblages mean X-values become reduced from about 8 to about 5. This reduction in the number of spiral chambers is accompanied by an increase in the mean protoconchal diameter from a level of 170 μ to one of 300 μ. The latter lineage was called the *carpenteri*-lineage by Tan as it perfectly fits to the recent species *C. carpenteri*.

Two evolutionary trends are recognized in the fossil and recent record of Indo-Pacific *Cycloclypeus*, i.e. a reduction in the number of spiral chambers and an overall increase in the size of the embryonic chambers. However, evolutionary change did not proceed in a steady and regular way.

I.2.3. The Mediterranean record

Cosijn (1938) investigated *Cycloclypeus*-bearing samples from the Oligocene of Spain. His most primitive assemblage contains specimens with long spires similar to Tan's oldest assemblage in the *koolhoveni*-lineage. In the successive samples of Cosijn the number of spiral chambers becomes reduced further than in the case of the *koolhoveni*-lineage, to a level which in Indonesia is recorded only in *C. eidae*. From Cosijn's data, however, no drop in protoconch-diameter is apparent. Protoconch-diameter shows but a slight increase in time. It varies at levels in between the large protoconch-sizes of the *koolhoveni* Cycloclypei and the small ones of *C. eidae*.

Because of these differences in evolutionary development and in protoconch-size Cosijn and later authors treated these Mediterranean Cycloclypei as separate species. Following the proposal of Matteucci and Schiavinotto (1985)

the assemblages of the Oligocene Mediterranean lineage are subdivided into two biometric species. Assemblages with mean X-values larger than 23 belong to *C. droogeri*, those with mean X-values smaller than 23 to *C. mediterraneus*. In the present monograph the lineage to which both species belong is referred to as the *droogeri*-lineage.

Drooger and Roelofsen (1982) reported the occurrence of an assemblage from the Upper Oligocene of Malta, which they determined as *C. eidae*. These Cycloclypei closely resemble the Indonesian species described by Tan. Drooger and Roelofsen considered *C. eidae* as an immigrant species in the Mediterranean realm. Although in Malta it was not found together with other Cycloclypei, these authors concluded from biostratigraphic data that an overlap with the range of *C. mediterraneus* cannot be ruled out. In that case advanced assemblages of *C. mediterraneus* would have occurred together with *C. eidae* in the Mediterranean in Late Oligocene times.

Cosijn (op.cit.) stated that in one of his samples specimens, ornamented with pustules were admixed to specimens with a smooth shell. In his other samples Cosijn recorded only these inornate morphotypes. According to the author the two types also differed in internal morphology and belonged to two different species and lineages.

Subsequently, MacGillavry (1962) supported this conclusion on the existence of two separate, contemporaneous and indigenous lineages in the Spanish Oligocene, which he called the Spanish ornate and the Spanish inornate lineage.

By contrast, in the views of Drooger (1955) and Drooger and Roelofsen (1982) differences in ornamentation in *Cycloclypeus* have no more than ecophenotypic significance. Smooth and ornate Cycloclypei would belong to one and the same lineage in which deeper living specimens would develop a pustulate external appearance in contrast to smooth, shallow-living specimens.

This suggestion was subsequently elaborated by Laagland (1988) studying the Cycloclypei of the Oligocene Ramla locality in Israel. The specimens in his material showed a variation in external test-morphology ranging from smooth to highly pustulate. No evidence was found in his data on internal and external morphology for the existence of more than one *Cycloclypeus* species (*C. mediterraneus*) in the Ramla material. Laagland furthermore concluded that, if a cline in *Cycloclypeus* existed at Ramla, with the more ornamented specimens living in the deeper parts of the depth-range, it was accompanied by a cline in internal morphology. In that case the size of the embryonic chambers as well as the number of nepionic chambers were different in successive depth-populations. This issue forms one of the major subjects of the present monograph and will be treated extensively.

I.3. PURPOSE OF THE INVESTIGATION

The purpose of our investigation was to gain more insight in the history of the genus *Cycloclypeus* in the Mediterranean realm during Oligocene times. The study comprises a number of topics.

The evolutionary development of the Mediterranean *droogeri*-lineage and the suggested immigration of *C. eidae* are treated in chapter IV. The biostratigraphic implications of these evolutionary and migrational processes are summarized in chapter VIII.

A second important topic comprises an evaluation of the taxonomic significance of ornamentation. We will try to establish whether ornate and inornate Mediterranean Cycloclypei belonged to two different contemporaneous species and lineages as proposed by Cosijn (1938) and MacGillavry (1962), or to a single lineage and species, which showed a depth-related cline in ornamentation, as suggested by Drooger and Roelofsen (1982) and Laagland (1988). We will furthermore investigate the relation between external and internal morphology in these Oligocene Cycloclypei to check whether there could have been a depth cline in internal morphology as well, as further suggested by these authors. These topics will be treated in chapters V, VI and VII. This part of the investigation includes a rather fundamental study on ontogenetic development in *Cycloclypeus* in an effort to improve our understanding of the parameters as well as the relation between these parameters which are usually measured and counted in *Cycloclypeus*.

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Chapter II

MATERIAL

II.1 SPAIN

Nearly all of our Spanish samples were collected from mass-transported bioclastic calcarenites and breccias, intercalated in marly deposits. *Cycloclypeus* is commonly associated with the larger foraminiferal genera *Pararotalia, Nummulites, Operculina, Heterostegina, Lepidocyclina* and *Amphistegina.* Miogypsinids are recorded in a restricted number of samples only. These samples are assigned to the *Miogypsinoides* Zone and all of the other *Cycloclypeus* bearing samples to the *Cycloclypeus* Zone of the Oligocene zonal scheme proposed by Drooger and Laagland (1986).

II.1.1 Alicante: Villajoyosa

Four samples were collected in the village of Villajoyosa and its direct vicinity (fig. 1).

Sample SP710 derives from the bank along the outer bend in the road northeast of the church, situated opposite the railway station of Villajoyosa (exposure 4 of Cosijn,1938). The sample was taken from a level of bioclastics, dispersed in a marly matrix, approximately 2 m stratigraphically below the base of a prominent limestone bed. It contains Lepidocyclinids which were determined as *Lepidocyclina (Nephrolepidina) morgani* (Mattheussens, int.rep.). Marls exposed somewhat more than 5 metres below the level of SP710, contain a nannofloral association indicative of Zone NP25 (Romein, int.rep.).

Sample SP707 was collected from calcarenites and bioclastic breccias exposed along the Rio Amadorio. Coming from the National Road N332, a secondary road, running south-west of the river, is followed in northern direction. The exposure is located 400 metres beyond the railway-bridge and directly southwest of the road. The sample contains an assemblage of very rare miogypsinids showing the highest mean number of spiral chambers recorded so far ($\bar{X}$: 28.0; see also table I). The assemblage is determined as *Miogypsina (Miogypsinoides) complanata.*

Samples SP724 and SP729 were taken along Cosijn's old cross-section along the road from Villajoyosa to Orcheta. After crossing the A7 motorway northwards in the direction of Orcheta, a series of massive, calcareous beds, dipping south, is exposed along the right side of the road. Some way back in the direction of Villajoyosa, the same series is exposed on the other side of the road

where it shows a northern dip. The material of sample SP729 was collected from both sites and derives from the coarse calcarenites and bioclastic breccias near the base of this series. Marls directly overlying these calcarenites, contain a nannofloral association indicative of Zone NP24 (Romein, int.rep.).

Further down the road to Orcheta, directly beyond the side road to the Pantano dam, a second series of massive, calcareous beds is exposed, dipping south. Sample SP724 was collected from the cross-bedded, bioclastic breccias in the basal part of the series, exposed at the right side of the road. The overlying marls, sampled at a level 1.5 m above the top of the series, may be assigned to the NP23/NP24 boundary interval (Romein, int.rep.).

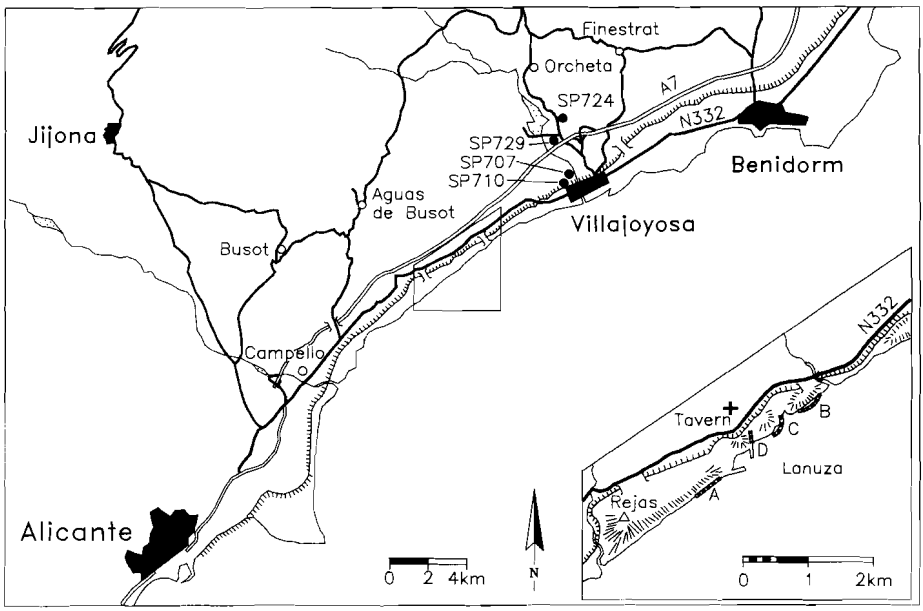

Figure 1: Schematic map of the Alicante region showing the location of the sampled sites.

II.1.2 Alicante: Lanuza

A total of 13 *Cycloclypeus* bearing samples was collected from a section along the coast between the villages of Villajoyosa and Campello (fig. 1). Along the National Road N332 from Benidorm to Alicante a tavern called Lanuza is situated on the right side of the road, at a distance of some 7 kilometres from the bridge over the Rio Amadorio and some 800 metres beyond kilometre stone 103. Turning left and crossing the railway track, the section is accessible by the road leading to a harbour at the base of the coastal cliffs.

The samples derive from calcarenites and bioclastic breccias which are intercalated in marly deposits. The sequence is exposed in a synclinal fold with a roughly E-W running fold-axis. The succession, reproduced in figure 2, is subdivided into four parts (see also inset in figure 1). Part A, comprising the base of the succession, is exposed in the southern limb of the fold, parts B and C in the northern limb and part D in the central part. Part D (SP836,SP839, SP841,SP842) is exposed in the cliff at the end of the road and directly above the pier on the north-eastern side of the harbour. Part C (SP825,SP827,SP831, SP835) is exposed in the cliffs north-east of the harbour, up to the next creek, part B (SP816,SP818,SP820) in the cliffs beyond this creek and part A (SP808,SP810) in the cliffs south-west of the harbour.

Parts A and B were correlated by means of two laminated marker-beds of blue, purple and yellowish, fine-grained calcarenites. Parts B and C were correlated by means of calcarenitic beds which can practically be traced from one part to the other. Between parts C and D the succession is not exposed. As part D is situated in the central part of the synclinal fold, it is thought to form the top of the sequence.

Very rare specimens of primitive *Miogypsinoides*-build are recorded at the levels of SP810, SP825, SP831, SP836 and SP841. They all seem to be microspheric and seem to form part of the variation range of the associated *Pararotalia viennoti*. The topmost sample SP842 contains an assemblage of very rare, primitive miogypsinids, which is assigned to *M.* (*Miogypsinoides*) *complanata* ($\bar{X}$: 24.8). According to data presented by Mattheussens (int.rep.) *Lepidocyclina* (*Nephrolepidina*) *praemarginata* is present in sample SP808 and an intermediate assemblage, labelled as *L. (N.)* ex. interc. *praemarginata-morgani*, in sample SP842.

The marly deposits in the succession were sampled at a number of levels. According to the planktonic foraminifera these samples derive from a continuous, 'time-progressive' section (Zachariasse, int.rep.). The samples in parts A and B (SP846-86, SP847,SP848,SP817), as well as sample SP850-86 near the base of part C, are assigned to Zone P21/N2. All of the other samples (SP822,SP826,SP851-86,SP832,SP838,SP946,SP947), from higher levels in the succession, are assigned to Zone P22/N3. The nannofloral associations in the samples from the marly intervals are indicative of Zones NP24/NP25 (Driever, int.rep.). The boundary between these two zones could not be recognized.

According to Verhallen (int.rep.) the benthic associations in the marly samples are dominated by relatively deep dwelling taxa (*Cyclogyra* spp., *Oridorsalis* spp., *Gyroidina umbonata*, costate buliminids, *Pullenia* spp.) The depositional depth of the basal part of the section (SP846-86, SP847) is estimated to be 1000 to 1200 metres, which is consistent with the P/B-ratios of about 25.

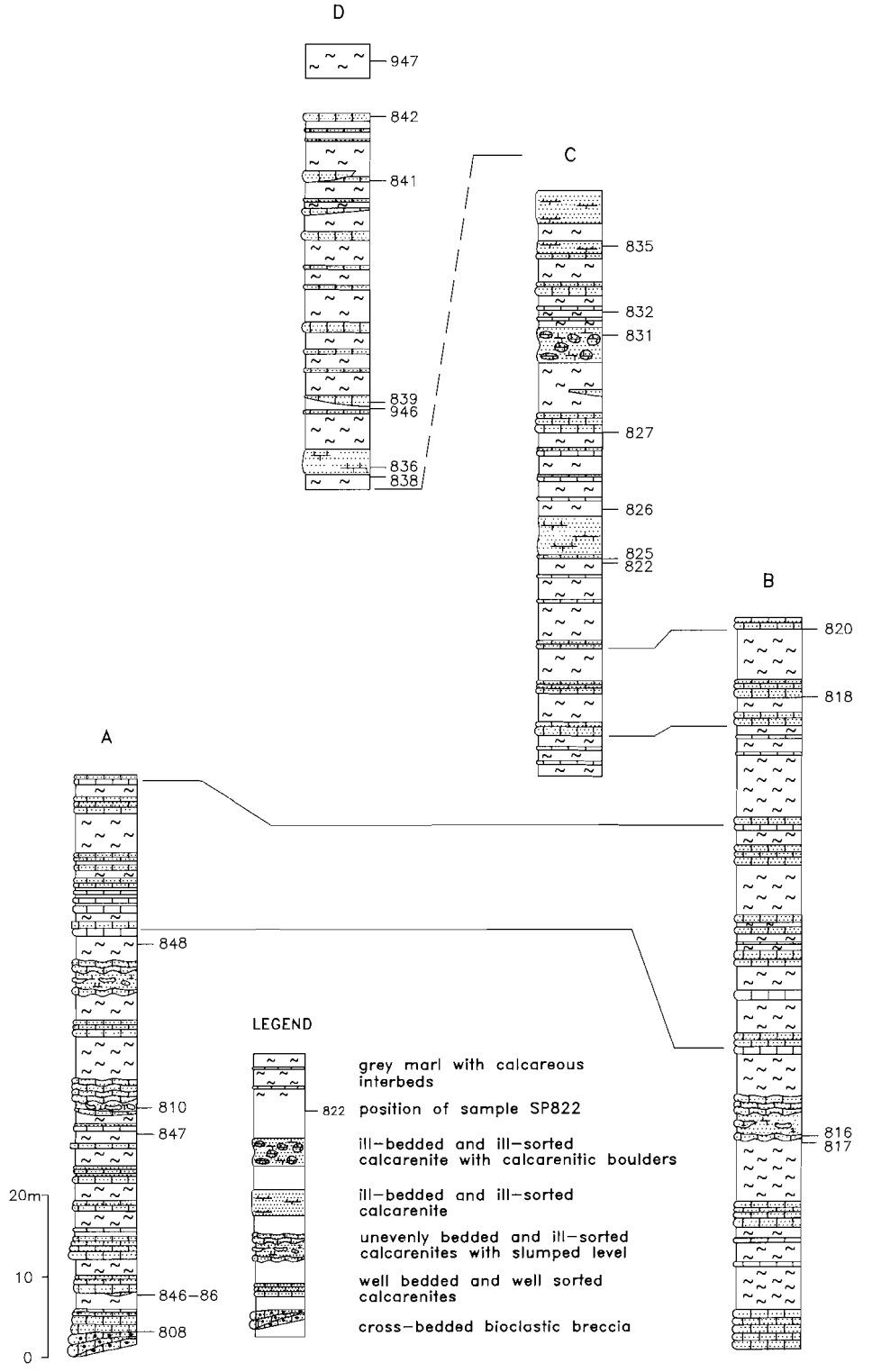

Figure 2: Lithological succession in the Lanuza section.

From sample level SP847 to sample level SP817 some shallowing is suggested by occurrences of *Gyroidina soldanii* and *Sphaeroidina* sp. in the associations and by a slight decrease of the P/B-ratios (20-24). However, as indicated by the presence of *Cibicides wuellerstorfi*, this shallowing presumably did not lead to depths of less than 1000 metres.

II.1.3 Granada: Navazuelo

The Navazuelo section is described by Gonzalez-Donoso et al. in Gelati and Steininger (1984). Coming from the National Road N324 from Jaén to

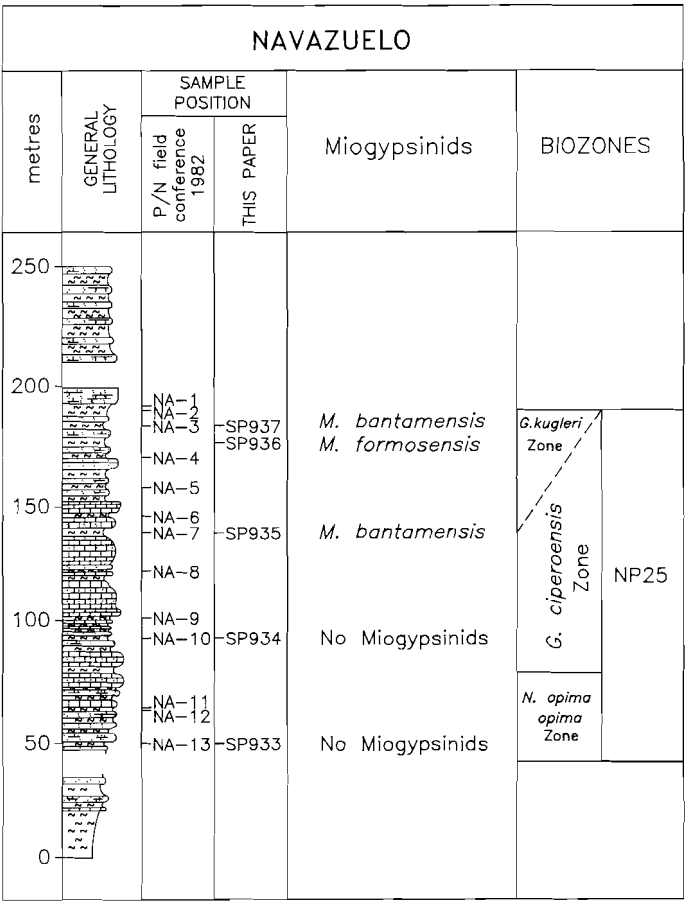

Figure 3: Lithological succession in the Navazuelo section and planktonic foraminiferal biozonation (after Gelati & Steininger, 1984) together with determinations of miogypsinid assemblages from the sampled levels.

Almería, a path is taken on the right side of the road, some 800 metres beyond the village limits of Guardahortuna. This path is followed for some 2100 metres. Turning right to the old farmhouse (Cortijo de Fuente de los Potros), the section is reached, which extends in southern direction along the mountain stream (Arroyo Pilates). It basically contains a succession of marls and calcarenites, gently dipping in southern direction. However, as the sequence is exposed rather badly, the lithological succession reproduced by Gonzalez-Donoso et al. (see figure 3) could not be recognized in the field. Fortunately, the earlier sampled sites were found to be marked with red paint. Our sample SP933 thus approximately corresponds to site 11 (NA-13) of the Spanish authors, SP934 to site 10 (NA-10), SP935 to site 7 (NA-7), SP936 to site 4.7 and sample SP937 to site 4.5 (NA-3).

Miogypsina (*Miogypsinoides*) *bantamensis* is recorded in samples SP935 and SP937 ($\bar{X}$: 10.6 and 12.4, respectively) and *M.* (*Miogypsinoides*) *formosensis* in sample SP936 ($\bar{X}$: 15.7).

According to the account of Biolzi et al. in Gelati and Steininger (op.cit.) no typical Miocene nannofossils are recorded in the marls of the Navazuelo section. All samples could be assigned to Zone NP25. In the same report Zachariasse et al. conclude that three planktonic foraminiferal zones can be recognized in the marls of the Navazuelo section. The basal part with the level of SP933 is assigned to the *Globorotalia opima opima* Zone (compare P21/N2), the middle part with SP934 to the *Globigerina ciperoensis* Zone (compare P22/N3) and the top of the succession is assigned to the *Globorotalia kugleri* Zone (compare N4). The boundary interval of the latter two zones would comprise the levels of SP935, SP936 and SP937.

II.1.4 Granada: other localities

Three localities were sampled along the N324 (Jaén to Almería), between the villages of Guardahortuna and Torrecardela. The sample site of SP939 is located some 3.4 kilometres from the village limit of Guardahortuna and some 350 metres before kilometre stone 179, in the right bank of a right bend following a relatively long stretch of straight road. The sample was collected from the base of an approximately 2 metres thick series of calcarenitic beds, intercalated in white marls.

The sample site of SP943 is located in the left bank of the road, some 20 metres before the second bend to the left after kilometre stone 179. The sample was collected from a 30 cm thick bed of coarse calcarenites intercalated in marls and contains an assemblage of *Miogypsina* (*Miogypsinoides*) ex. interc. *formosensis-bantamensis* ($\bar{X}$: 12.5).

Sample SP938 was taken from a relatively coarse level in the middle of an approximately 1 metre thick calcarenitic bed. This bed crops out in the left bank of the road, some 650 metres beyond kilometre stone 179. The sample contains an assemblage of *M.* (*Miogypsinoides*) *formosensis* ($\bar{X}$: 13.6).

II.2 ITALY

Sample JT7911 was collected at the type locality of *Cycloclypeus droogeri* and *C. mediterraneus* near L'Aquila (Italy) and from the type level of the latter species in the top part of the local succession (Matteucci & Schiavinotto, 1985). At this level, rich in larger foraminifera dispersed in a grey, marly matrix, Matteucci and Schiavinotto (1977,1985) recognized furthermore lepidocyclinids (*L.* (*Eulepidina*) *dilatata* and *L.* (*Nephrolepidina*) *morgani*), *Operculina, Heterostegina, Amphistegina* and very rare *Miogypsina* (*Miogypsinoides*). Also in our material miogypsinids are very rare; they are of primitive build, showing a large number of spiral chambers ($\bar{X}$: 22.6). The assemblage is determined as *M.* (*Miogypsinoides*) *complanata*. The level of JT7911 was referred to Zone N3 (Matteucci & Schiavinotto, 1977) and is assigned to the base of the *Miogypsinoides* Zone of Drooger and Laagland (1986).

II.3 ISRAEL

Samples IR469 and IR470 were collected from grey, clayey marls exposed in the Ramla locality in Israel. As reported by Drooger (1986) *Cycloclypeus mediterraneus* is associated in these deposits with other larger foraminifera of the genera *Lepidocyclina* (*L.* (*Eulepidina*) sp. and *L.* (*Nephrolepidina*) *praemarginata*), *Amphistegina, Pararotalia, Nummulites, Operculina* and *Heterostegina*. These larger foraminifera, together with other shallow water elements, are found admixed with more open marine species. Drooger therefore concluded that these sediments accumulated in a muddy, offshore environment to which a large number of allochthonous elements had been added from shallower waters.

The Ramla deposits were referred to Zone P21/N2 and to Zone NP24, as indicated by the planktonic foraminiferal and nannofloral associations, respectively (Drooger, op.cit.). Drooger and Laagland (1986) assigned these deposits to their *Cycloclypeus* Zone.

II.4 CHRONOSTRATIGRAPHY

In the earlier sections of this chapter a fair number of our larger foraminiferal

associations were correlated with the zonal schemes based on planktonic foraminifera and calcareous nannofossils. These new data allow for a more accurate calibration of the zonation of Drooger and Laagland (1986), based on larger foraminifera from the European-Mediterranean region.

In our revised version, presented in figure 4, the planktonic zonations and numerical time-scale are largely adopted from Berggren et al. (1985). The figure

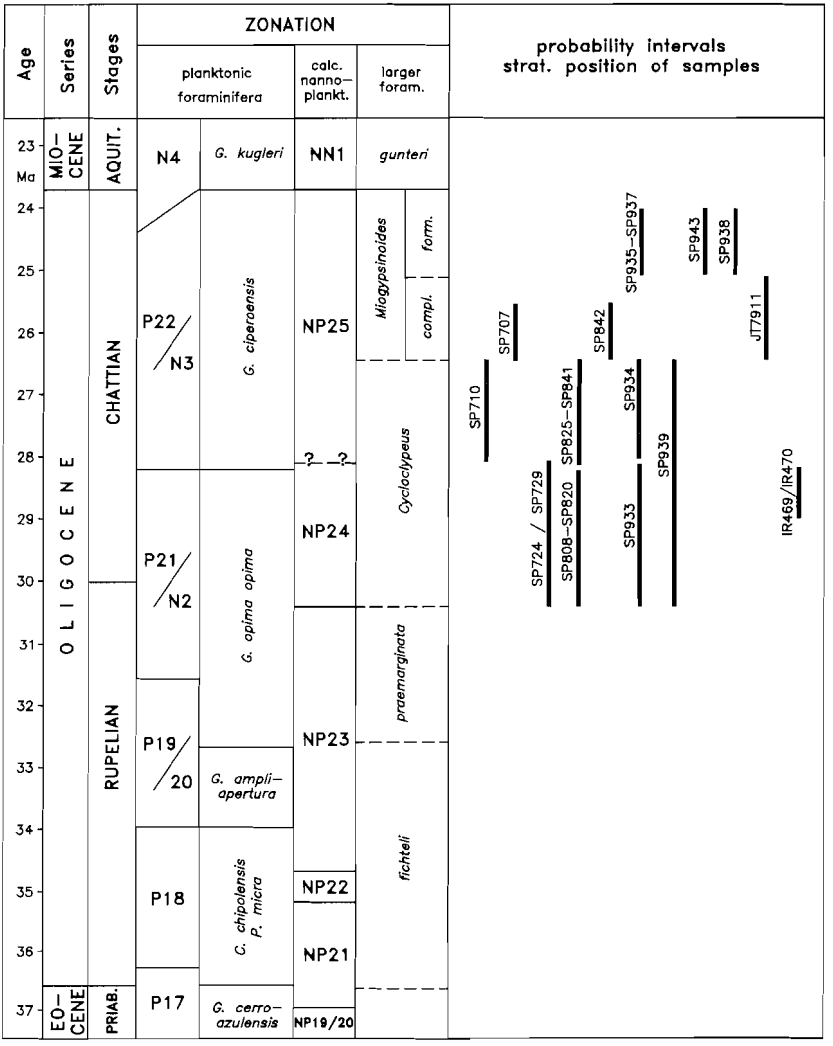

Figure 4: Biostratigraphic scheme (revised after Drooger & Laagland, 1986) with estimated stratigraphic intervals from which our samples derive.

furthermore shows our estimates for the stratigraphic intervals from which our samples with larger foraminifera derive. According to these estimates our samples derive from the interval from the top of the Lower Oligocene (Rupelian) to the top of the Upper Oligocene (Chattian). In chapter VIII the zonal scheme will be supplemented with the data on *Cycloclypeus* and further reviewed (fig. 60).

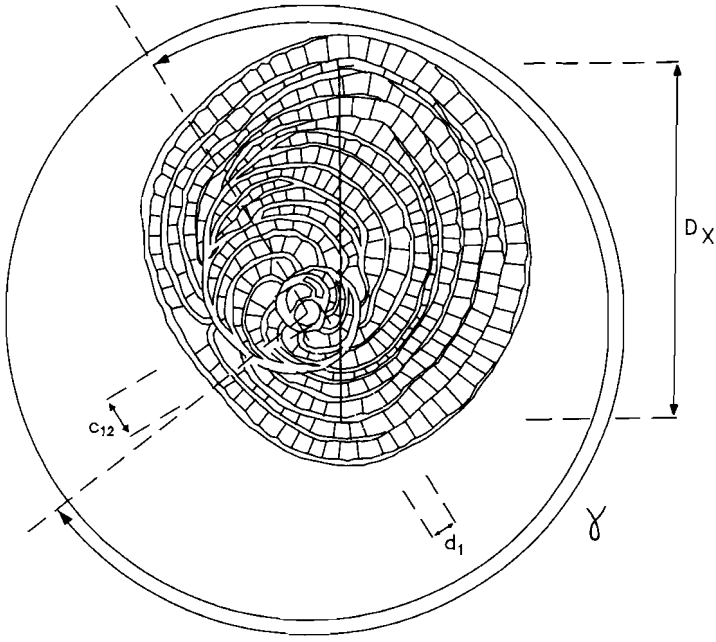

Figure 5: Chamber arrangement of *Cycloclypeus* in median section. Parameters d_1, c_{12}, γ and D_x are determined as indicated. γ = 620° and X = 19.

Chapter III

METHODS

In all of our European samples *Cycloclypeus* is very rare. Large quantities of residue, in the 0.85-4.00mm fraction, had to be looked over to obtain sufficient numbers of specimens for our morphometric analyses. In the residues of our samples from Israel *Cycloclypeus* is more abundant.

In a number of samples Cycloclypei were studied both externally and internally. In these studies only well preserved and large specimens were used.

After inspection of the external features the specimens were sectioned. During the subsequent biometric study of the internal morphology, the annotations on the external morphology were kept apart to minimize bias in the conclusions on interrelations.

The following parameters were determined in all of the samples investigated (fig. 5):

d_1: Maximum internal diameter (in μ) of the protoconch perpendicular to the medio-embryonic line.

c_{12}: Maximum internal diameter (in μ) of the protoconch and deuteroconch together measured along the medio-embryonic line.

X: The number of precyclic chambers; the embryonic chambers are included in the count, whereas interpolated chambers, i.e. chambers without an 'apertural chamberlet', are not.

γ: The number of convolutions in the spiral stage, expressed as the angle in degrees of arc between the line from the centre of the protoconch through the centre of the deuteroconch and a second line connecting this protoconchal centre with the anterior end of the chamber lumen of the last chamber in the X count. γ values of 360° and larger are measured in specimens showing at least one complete nepionic whorl.

Parameters d_1 and c_{12} are estimates for the size of the embryon. So far the embryonic stage in *Cycloclypeus* was considered to comprise the protoconch and deuteroconch only. Frequently, however, these two chambers appear to constitute a separate morphological unit together with the third chamber, as these three early chambers together are surrounded by a relatively thick wall. The embryonic stage in the ontogenetic development of our Cycloclypei is therefore considered to be represented by these first three chambers.

The angle of parameter γ was introduced (Laagland,1988) as an alternative to the classic nepionic parameter X. This number cannot be determined when part of the suite of spiral chambers is obscure in the thin sections. Parameter

γ is expected to be less sensitive in this respect and therefore may be helpful when whole-rock thin sections are studied or in studies of samples with badly preserved specimens or with numerous specimens showing an undulating test.

In a restricted number of samples the maximum diameter of the precyclic stage was determined. This parameter, introduced as D_X and measured in mm., includes the thickness of the wall of the last chamber of the X count.

In our samples from Ramla, Israel, a number of additional parameters were determined. Various features of the early ontogenetic development in *Cycloclypeus* individuals were measured (fig. 6). The suffix i in these parameters refers to the ordinal number of the chambers in the X count. With the aid of a digitizing tablet measurements were performed from drawings of the thin sections, which were copied from film negatives (magn. 100 ×).

L_i: Length (in mm.) of chamber i measured over the middle of the septal wall and extending to the outer margin of the marginal cord at the posterior end of the chamber lumen.

O_i: Perimeter (in mm.) of the test at stage i. The measurement proceeds as described for parameter L_i and is extended along the remainder of the outer margin of the test at stage i.

E_i: Degree of embracing of chamber i as estimated by the ratio L_i/O_i. Parameter E_i is recorded as a percentage.

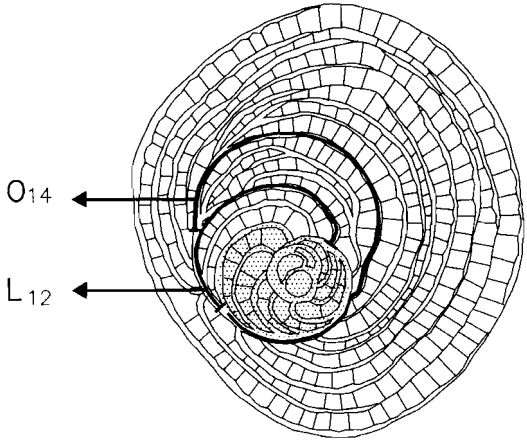

Figure 6: *Cycloclypeus* in median section. Shaded: area of the test in median section at stage i = 10. The length of the 12th chamber (L_{12}) and the perimeter of the test at stage i = 14 (O_{14}) are measured as indicated.

A_i: Surface (in mm^2) of the test in median section at stage i. This area is bounded by the perimeter of the test at this stage as defined in the description of parameter O_i.

k_i: Relative size increase of the test at stage i, being the surface area of the test in median section at stage i relative to the area in the preceding stage i-1 (A_i/A_{i-1}). Parameter k_i is recorded as a fraction.

The measurements on parameter L_i serve only to calculate the degree of embracing E_i and are not presented separately.

Axial sections show an evolute arrangement of the chamber lumina and only little variation in chamber height (h) in the Ramla specimens. Therefore differences in the values of parameter A_i are thought to reflect primarily differences in the total volume of the chambers at stage i (V_i). In that case parameter k_i is an estimate of the volume at stage i relative to that of the preceding stage. In simplified version:

$$\frac{V_i}{V_{i-1}} = \frac{A_i \times h}{A_{i-1} \times h} = k_i$$

Thus k_i is thought to be a reflection of the relative increase in chamber volume at each stage i, which in turn is thought to be proportionate to the relative increase of the protoplasm volume in this growth step.

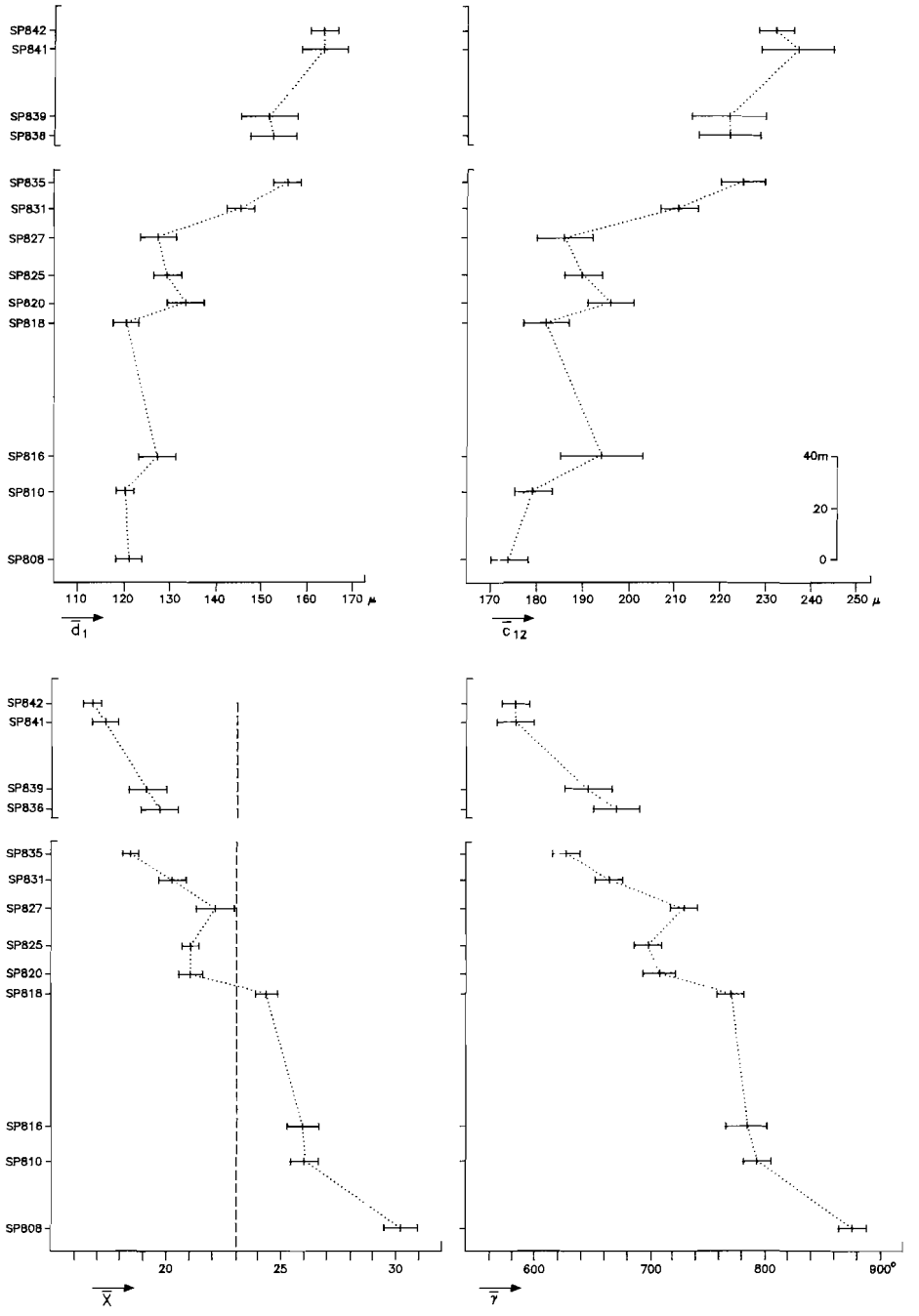

Figure 7: Mean values (± 1 SE) of parameters d_1, c_{12}, X and γ in section Lanuza.

Chapter IV

INTERNAL MORPHOLOGY

In this chapter we will present the data on parameters d_1, c_{12}, X, γ and D_X which measure various internal features of our Cycloclypei. The data on D_X will be presented in a separate section at the end of the chapter as the results on this parameter are based on a restricted part of the sample set only.

IV.1 PARAMETERS d_1, c_{12}, X AND γ

The biometrical data of single samples were arranged in histograms and scatter diagrams. In most of our samples no distinct evidence was found for heterogeneity. The few exceptions will be discussed separately; each of the other assemblages is considered to be constituted by more or less time-equivalent representatives of a single species-unit, although probably all samples contain more or less allochthonous microfossils.

IV.1.1 Spain: Alicante

The Lanuza Section

For the Lanuza samples mean values ($\pm$ 1 SE) of parameters d_1, c_{12}, X and γ are presented in stratigraphic order in figure 7 and listed, together with associated statistics, in Table II. Figure 7 illustrates an upward increase in the mean size of the embryon and a simultaneous decrease in the mean number of precyclic chambers and in the mean number of convolutions. This seems to confirm conclusions on trends reached earlier by Cosijn (1938) and Drooger and Roelofsen (1982) and seems to correspond to similar trends in mean values of d_1 and X in lineages of Indonesian *Cycloclypeus* described by Tan (1932). All of these authors ascribed these trends to evolutionary processes. On this we agree, as these trends can be traced in different areas in more or less corresponding time intervals, irrespective of the type of sediment involved. The change in nepionic configuration leads from an Oligocene, largely spirally arranged morphology, which is very close to the one of the ancestral *Heterostegina* species, to the almost entirely cyclical build of the Recent representatives of *Cycloclypeus* in the Indo-Pacific.

Our biometrical study of the Lanuza section offers the opportunity to study the course of the morphological development in some detail. Figure 8 contains the frequency distributions of parameter X in the successive assemblages. It

shows that in the assemblages from higher stratigraphic levels variants with progressively smaller numbers of spiral chambers are introduced. Simultaneously the primitive variants with numerous spiral chambers decrease in numbers and disappear.

Also the sequence of mean values of X in figure 7 gives the general impression

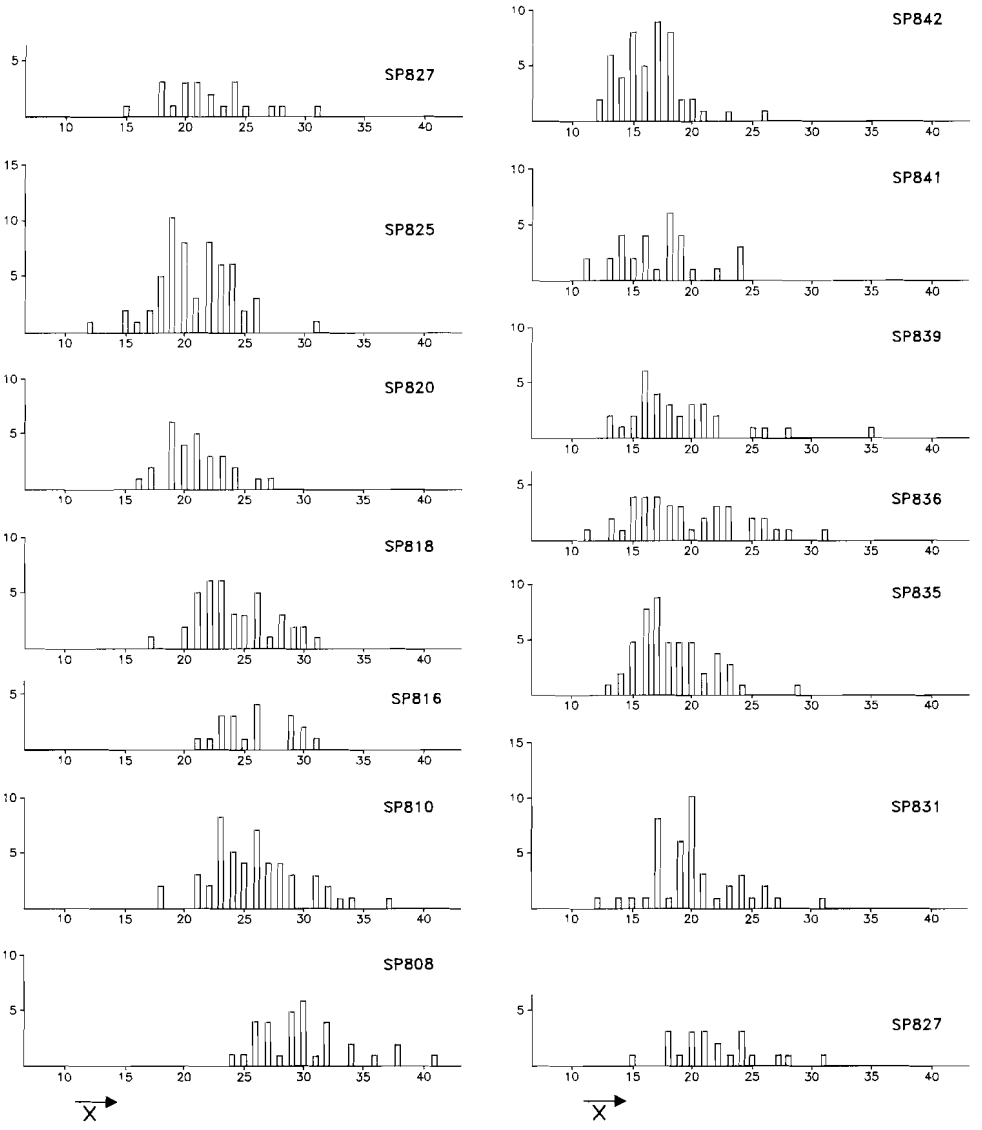

Figure 8: Frequency distributions of parameter X in the samples from Lanuza.

of a progressive reduction of the number of precyclic chambers in the stratigraphic succession. No statistically significant 'backward' leaps or pulses are apparent in the morphological record as in the case of the Miocene *Planorbulinella* from Crete (M.M. Drooger et al.,1979). From sample level SP818 to that of SP820 the morphological change in 'forward' direction seems to be disproportionately large with respect to the small lithostratigraphic interval involved. If evolution were gradual and showing a constant rate of change, this 'leap' might be due to an important reduction in the sedimentation rate for this part of the sequence or even to an interruption in the lithological record. However, there is no field evidence in the homogeneous marls in between both sample levels, supporting either one or the other of these possibilities.

Alternatively, a morphological gap or a distinct increase in the rate of nepionic evolution might be inferred. Actually, the reduction of the number of spiral chambers at this level coincides with the transition from *C. droogeri* to *C. mediterraneus*, two biometrical species described by Matteucci and Schiavinotto (1985). Transitional assemblages were not represented in the Mediterranean Oligocene record at that time and our newly acquired data can only partly fill this gap. So, the morphological break between the levels of SP818 and SP820 may be of more than local significance.

These data on the classic parameter X are nicely congruous with those on parameter γ, which was introduced only recently (Laagland,1988). The angle γ therefore seems to be a successful alternative in estimating the level of nepionic development of *Cycloclypeus* when data on X are wanting.

The reduction of the nepionic stage in the Lanuza succession is accompanied by an upward increase of mean embryon-size values. This increase in the embryon-dimensions is more distinct in the successive assemblages of *C. mediterraneus* than in those of *C. droogeri*. Furthermore the assemblages can be arranged into two series: the lower one with relatively small mean embryon-diameter values (d_1 below 140 μ) and the other one comprising the upper assemblages with larger values. However, this subdivision does not correspond to the previous one based on the nepionic characters. The 'discontinuity' level does not occur between the levels of SP818 and SP820, as in the case of the nepionic development, but rather between the levels of SP827 and SP831. Both the lower and upper sequence of assemblages would show an overall increase in mean embryon-dimensions. As in the case on the nepionic development the change in embryon-diameter from SP827 to SP831 is not readily explained by a gap in the record or a decrease in sedimentation rate. Since we do not find a similar large change in the nepionic arrangement at this level of the succession, the change in embryon-size may reflect a biological rather than a geological phenomenon.

In Table III correlation coefficients are listed for four parameter combinations. Strong, positive correlations are observed for the d_1-c_{12} and X-γ combinations. Weaker, but usually still significant, negative correlations exist for the d_1-X and d_1-γ combinations. These results are characteristic for all of our *Cycloclypeus* assemblages investigated.

Villajoyosa

The *Cycloclypeus* assemblage in the locality of Villajoyosa station seems to be heterogeneous in composition as was already shown by Cosijn (1938). As this author ascribed the heterogeneity to the co-occurrence of ornate and inornate specimens in this assemblage, the biometric data on our sample from this locality (SP710) will be presented in chapter V, dealing with the relations between external and internal morphology.

The results on the other three samples from this area are listed in Tables IV and V (univariate and bivariate analysis, respectively). Samples SP724 and SP729 from the vicinity of Moli de Llinares contain assemblages of *C. droogeri* ($\bar{X}$: 31.3 and 28.6, respectively). Cosijn reported similar primitive Cycloclypei from his sample 455 from the same section. The specimens in our sample SP707 from the river bank in Villajoyosa are more highly developed and referable to the other species of the Mediterranean lineage: *C. mediterraneus* ($\bar{X}$: 17.6).

IV.1.2 Spain: Granada

The statistical results on the *Cycloclypeus* samples from the Granada province are listed in Tables VI (univariate analysis) and VII (bivariate analysis). Some of these results, on the Navazuelo samples, are also incorporated in figure 9. The lower two of the Navazuelo samples contain *C. droogeri* (SP933 $\bar{X}$: 26.9) and *C. mediterraneus* (SP934 $\bar{X}$: 20.2). In the upper three samples (SP935,SP936,SP937) *C. eidae* is present ($\bar{X}$: 17.2, 18.2 and 18.4, respectively). The latter species is easily recognized by its relatively small embryon-dimensions ($\bar{d}_1$: 85 - 90 μ). In the other Granada samples, from the direct vicinity of the Navazuelo section, assemblages of *C. eidae* are present as well (SP938 $\bar{X}$: 19.1 and SP943 $\bar{X}$: 18.0). Another assemblage of *C. droogeri* is present in SP939 ($\bar{X}$: 24.4).

The *eidae* assemblage of SP935 from Navazuelo contains three specimens with very large embryons and few spiral chambers. This is illustrated by the frequency distributions in figure 10 and the scatter diagrams in figure 11. If these specimens would belong to *C. mediterraneus*, we were to expect more distinct morphological differences in external appearance, as *C. mediterraneus* is quite robust in appearance compared to the more delicate features of *C. eidae*

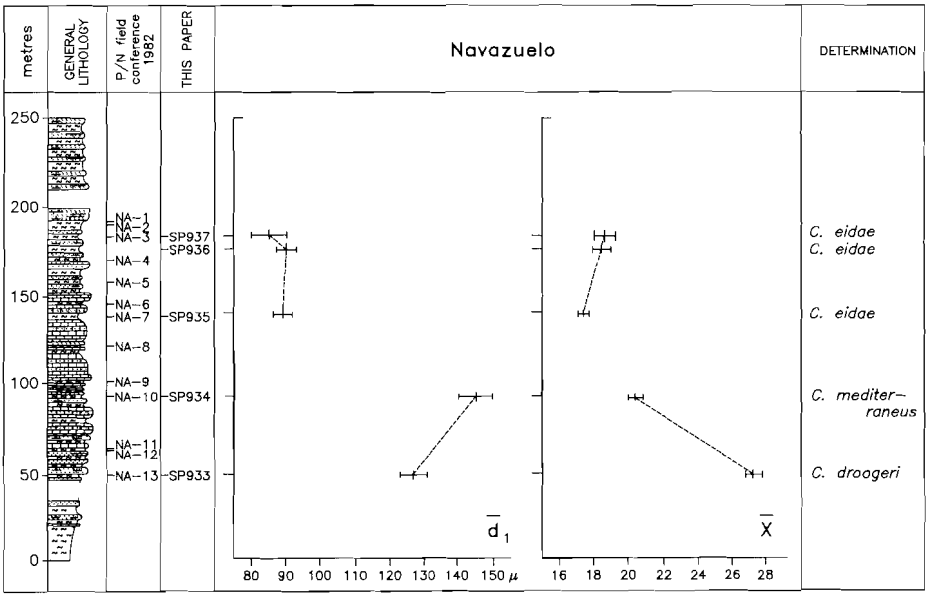

Figure 9: Mean values (± 1 SE) of parameters d_1 and X in the samples from Navazuelo.

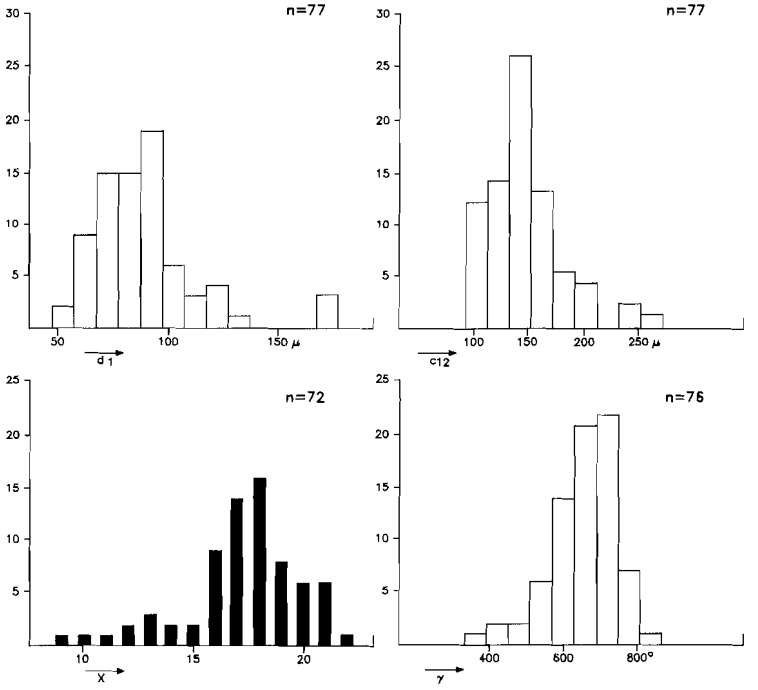

Figure 10: Frequency distributions of parameters d_1, c_{12}, X and γ in sample SP935.

(see also chapter V). Internally, the mesh-work of chamberlets in *C. eidae* is more delicate as well, which is most distinct in the nepionic part of the test (plate 9, fig. 3). In the three exceptional specimens of SP935 the embryonic chambers are large but the subsequent chambers and chamberlets have the delicate build, characteristic of *C. eidae*. Actually, there is one other specimen in the sample that shows the coarse mesh of chamberlets of the *droogeri* lineage. As this specimen was also badly preserved, it is provisionally considered to be an element of this lineage, reworked from older strata. In each of the scatter diagrams of figure 11 the data on this specimen, marked with an asterisk, form part of the main cluster.

In two of the three specimens with large embryons the number of precyclic chambers is also unusually small (9 and 10) for *C. mediterraneus*. This deviation is illustrated in the scatter diagram of d_1 versus X in figure 12, in which the observations on the SP935 assemblage are plotted together with those on SP808 (*C. droogeri*) and SP842 (*C. mediterraneus*) from the Lanuza section. At similar

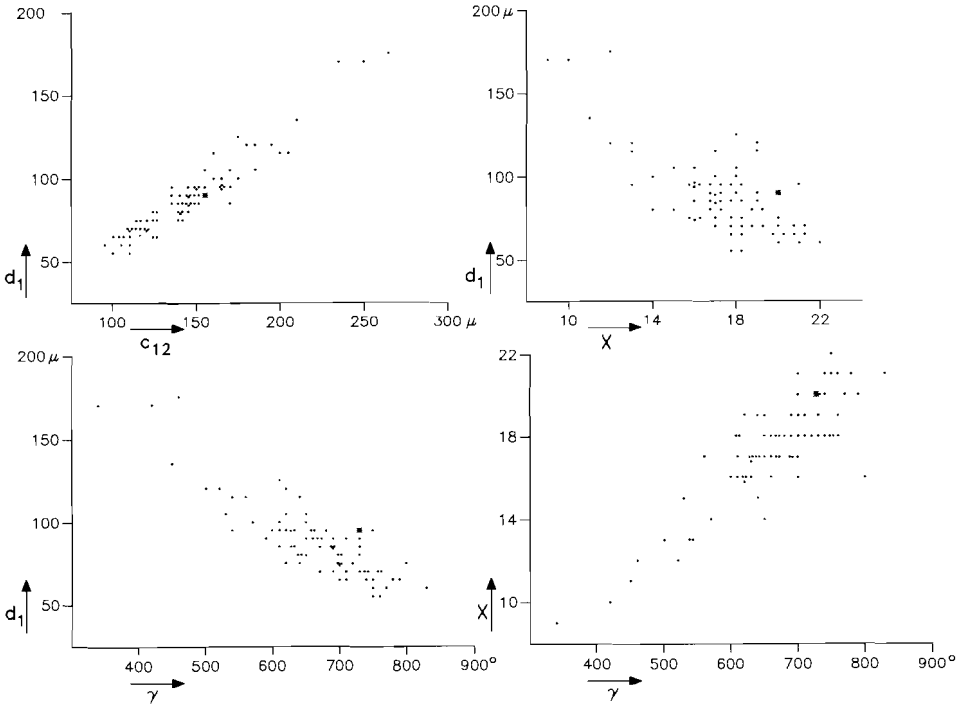

Figure 11: Scatter diagrams of data on selected parameter combinations in sample SP935. Asterisk refers to presumably reworked specimen.

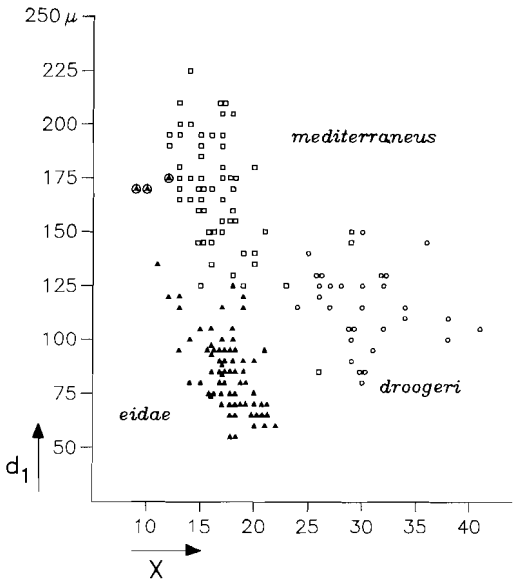

Figure 12: Scatter diagram of data on parameters d_1 and X from samples SP808 (*C. droogeri*), SP842 (*C. mediterraneus*) and SP935 (*C. eidae*). Data on '*carpenteri*-types' encircled.

size of their embryons the *eidae* specimens of SP935 tend to have relatively smaller numbers of spiral chambers than the *droogeri* and *mediterraneus* specimens. In this respect the two or three extraordinary specimens from SP935 form no exception and therefore it seems the more difficult to refer these specimens to *C. mediterraneus*.

It is more likely that we are dealing with a phenomenon which we know quite well from the Indonesian region. There *C. eidae* ranges up into the Miocene where it is accompanied initially, as in SP935, by rare specimens with very large embryons and small numbers of spiral chambers. As this latter group steadily increases in relative numbers, clearly bimodal distributions are recorded in d_1 and X and eventually *C. eidae* disappears entirely from the record. In the concept of MacGillavry (1962) the surviving Cycloclypei belong to the *carpenteri* lineage, which would have originated from the *eidae* lineage by some sort of saltative evolutionary process.

Earlier, Drooger (1955) suggested that the *eidae*-types are microspheric specimens; they would constitute a single species together with the *carpenteri*-types, which would represent the megalospheric generation. As most of our own *eidae*-morphotypes have embryonic chambers which are clearly too large in size to be microspheric, the option of Drooger does not seem to be realistic. We are reluctant, however, to treat the two types as separate, genetically

isolated species, as suggested by MacGillavry. Therefore the few exceptional individuals in our Spanish Oligocene assemblage of SP935 are not formally labelled. The specimens are referred to as the *carpenteri*-types, as distinguished from the *eidae*-types.

The biometrical results on the assemblage of SP935 in Tables VI and VII are based on the *eidae*-types and *carpenteri*-types together and on one specimen, provisionally assigned to the *droogeri* lineage. For the *eidae*-types alone the results would be:

	N	M	SD	SE	V
d_1 (μ)	73	86	18	2	20.5
c_{12} (μ)	73	142	27	3	18.8
X	68	17.5	2.3	0.3	12.9
γ (°)	72	670	75	9	11.1

d_1-c_{12}	d_1-X	d_1-γ	X-γ
r = 0.93	r = -0.58	r = -0.80	r= 0.79
N = 73	N = 68	N = 72	N = 68

Although the r values are slightly smaller than the corresponding values in Table VII, all correlations are still highly significant ($p < 0.01$).

For the three *carpenteri*-types in SP935 the mean parameter values would be:

$\bar{d}_1$: 172 μ $\bar{c}_{12}$: 250 μ $\bar{X}$: 10.3 $\bar{\gamma}$: 410°

All three Mediterranean *Cycloclypeus* species were found in the Navazuelo set of samples (fig. 9). Assemblages of the *droogeri* lineage are succeeded by assemblages of *C. eidae*. This is in agreement with the conclusions of Drooger and Roelofsen (1982) and Drooger and Laagland (1986) about the stratigraphic succession of these species in the Mediterranean region. However, as no distinct, mixed *mediterraneus-eidae* assemblages were recorded, we cannot document the overlap in the ranges of both species suggested by the latter authors. Such an overlap would occur in the stratigraphic range of *Miogypsinoides complanata*. The absence of this species in Navazuelo hints, however, to a gap in our sample record. This gap would include the *Miogypsinoides complanata* Subzone of the tentative zonal scheme presented by Drooger and Laagland (op.cit.).

If the observations on the few *carpenteri*-types in SP935 are left out of consideration, no significant differences are recorded in any of the parameters in the suite of *eidae* assemblages from Navazuelo. Therefore little can be said

about possible evolutionary changes in this *Cycloclypeus* species in the interval covered by our samples.

IV.1.3 Localities outside Spain

The statistical results of the Italian and Israelian samples are listed in Tables IV and V (univariate and bivariate analysis, respectively). The data on our Cycloclypei from the type locality of *C. mediterraneus* near L'Aquila, Italy, closely resemble those published by Matteucci and Schiavinotto (1977), although according to our estimate the mean protoconch-diameter would be slightly larger ($\bar{X}$: 16.6 (M&S) vs. 16.1; $\bar{d}_1$: 133 μ (M&S) vs. 149 μ).

Data on our sample IR469 from Ramla, Israel, were published earlier (Laagland,1988). The observations on this sample and those on sample IR470 from the same locality, were lumped as no significant differences could be established. Our mean X value of 20.2 agrees fairly well with the results of earlier studies on the *C. mediterraneus* assemblages from this locality, which were published by Drooger (1986). However, our estimate of the mean protoconch-diameter (164 μ) is a little larger than the earlier ones of Drooger (147 - 152 μ). This deviation bears resemblance to that of the previous case on the Cycloclypei from L'Aquila. In the present case, however, our relatively large protoconch-size estimate may be due to a difference in the procedure of the investigation. Instead of measuring all specimens present in a random split of the residue, we measured large, well preserved specimens only.

To check whether this could have caused the difference, we additionally measured a fair number of small and badly preserved Cycloclypei, left over in the residue of sample IR469. However, similar large values were found for the mean embryon dimensions. So, we have to look for some other reason to explain the apparent consistency in the differences of our embryon-size estimates with those published by Drooger.

We think such a reason may be found in the difference in the method of preparing the specimens. Our measurements are probably more accurate as these were performed on thin-sectioned individuals, whereas Drooger's results are based on observations on half-sectioned specimens only. Moreover, the inner walls of the chambers and chamberlets of the Ramla Cycloclypei are frequently overgrown by secondary calcite. In cross-section it can be clearly observed that the inner walls of such specimens are covered by a rim. Half-sectioned specimens have to be studied under incident light in which case, however, no distinction can be made between the original wall and its secondary thickening. Therefore the recorded diameter of the protoconch would be consistently too small in half-sectioned specimens with overgrown inner walls.

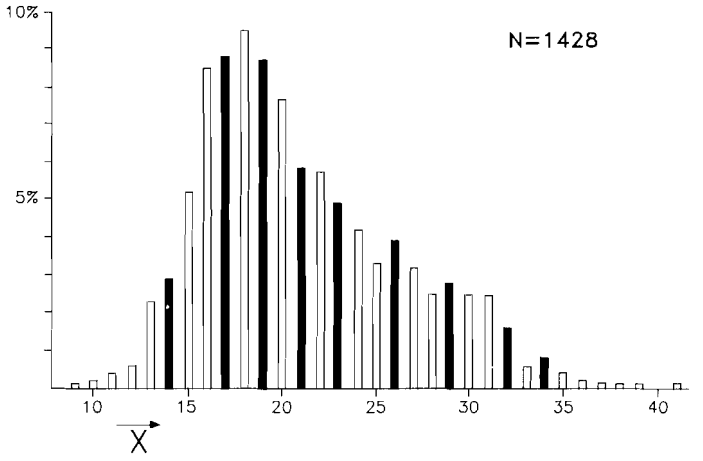

Figure 13: Frequency distribution of all X-observations together except for those from SP710. Shaded bars: X-variants regarded as 'elementary species' by Tan.

IV.1.4 Compilation

In the X-distributions of *Cycloclypeus* samples from Indonesia Tan (1932) observed a predominance of a number of variants with specific X-values. This predominance of X-variants, which Tan called elementary species, could not be recognized by Cosijn (1938) in his samples from the Spanish Oligocene, nor by Drooger (1955) in samples from the Indonesian Miocene. In the X-distributions of our Mediterranean assemblages no predominance of particular X-variants can be observed either. This is corroborated by the distribution in figure 13 (Table VIII) which includes all of our observations on parameter X with the exception of those from sample SP710 from Villajoyosa. We agree with Cosijn and Drooger that Tan's polymodal X-distributions may be largely the result of subjective judgement.

In the scatter diagrams of figures 14 to 17 an overview is presented of the biometric data on Oligocene *Cycloclypeus*. The mean parameter values of our samples are plotted together with those from other studies. Samples indicated by SP- and JT- codes are part of the present investigation. With regard to the other labels the reader is referred to the data presented below.

- Moli (de Llinares), Ronda, Jaèn, Villa(joyosa) (fig. 15): Spain, Cosijn, 1938. The data on the mean protoconch-diameter of the first three of these Spanish assemblages were taken from a later report by Cosijn (1942). The mean values of the Villajoyosa assemblage are based on lumping of Cosijn's data on ornate and inornate Cycloclypei.

- L'Aq(uila)-1, L'Aq(uila)-2 (fig. 15): Italy, Matteucci and Schiavinotto, 1977.
- Mollere (fig. 15): Italy, Meulenkamp and Amato, 1972.
- Sicily (fig. 15): Italy, Wildenborg (in prep.)
- Malta (fig. 15): Drooger and Roelofsen, 1982.
- Corfu (fig. 15): Greece, de Mulder, 1975.
- Ramla (figs. 14-17): Israel, this paper.
  Mean values are based on the lumped data set of samples IR469 and IR470. W and Z (fig. 15) refer to data on Cycloclypei from the same locality published by Drooger (1986).
- Bantam (fig. 15): Indonesia, Tan Sin Hok, 1932.
  Samples containing assemblages of the *koolhoveni* lineage from the localities Tjimanggoe and Tjiapoes.
- Tjim(anggoe) and Tjiap(oes) (figs. 14-17): Indonesia, Kesseler (int.rep.) and Okkes (int.rep.), respectively.
  The latter two samples were derived from the localities of Tan but not necessarily from the same strata.
- Borneo (fig. 15): Indonesia, Tan Sin Hok, 1932.

In the scatter diagram of $\bar{d}_1$ versus $\bar{c}_{12}$ (fig. 14) the *eidae* assemblages constitute a separate cluster due to their small embryon dimensions. The

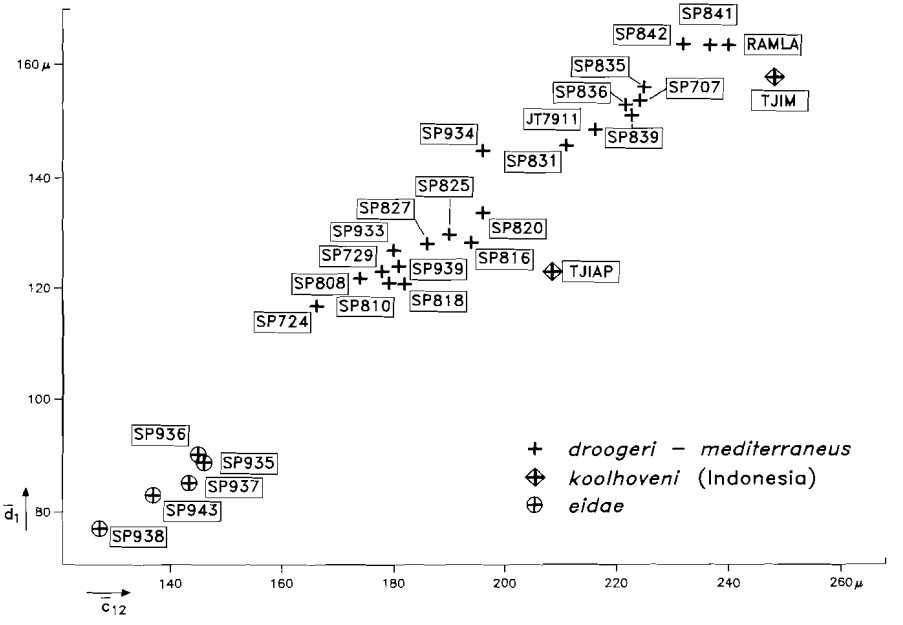

Figure 14: Scatter diagram of mean values of parameters d_1 and c_{12}.

assemblages of the *droogeri* lineage do not form a continuous cluster as a distinct morphological break is apparent at a mean protoconch-diameter of 140 μ. This gap was already traced in the suite of assemblages from Lanuza. It has been argued already that the morphological gap in the records of $\bar{X}$ and $\bar{\gamma}$ values from the same succession was of more than local significance. This may apply to the gap in mean protoconch-diameter as well.

Another gap may be present at a mean protoconch-diameter of 160 μ, separating the Ramla samples and the upper two Lanuza samples from the other assemblages. However, this gap in the morphometrical record may well be due to chance in view of the restricted number of data in this part of the diagram.

The two *koolhoveni* samples from Indonesia (from the internal reports) plot to the right of the assemblages of the *droogeri* lineage, which points to a difference in the relation between $\bar{d}_1$ and $\bar{c}_{12}$. In assemblages with corresponding mean protoconch-diameters the Indonesian Cycloclypei have a larger mean value for the diameter of the protoconch and deuteroconch together and therefore a larger mean size of the deuteroconch.

In the scatter diagram of $\bar{d}_1$ versus $\bar{X}$ (fig. 15) the assemblages of the *droogeri* lineage become arranged in two clusters because of a gap in the $\bar{X}$ record in between the values of 22 and 24. This morphological gap straddles the boundary between the two biometric species of this lineage, set at the mean X value of 23. In the cluster of *mediterraneus* assemblages the reduction in the mean number of precyclic chambers is on the average clearly associated with an in-

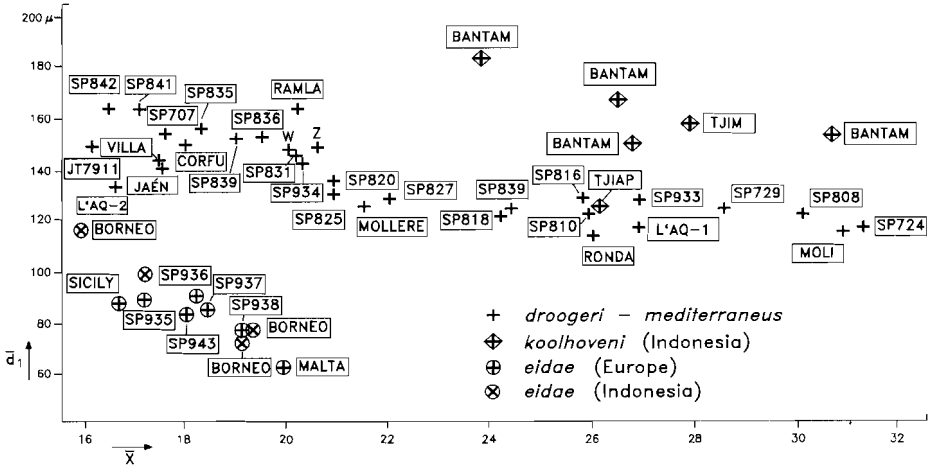

Figure 15: Scatter diagram of mean values of parameters d_1 and X.

crease in mean protoconch-diameter. This is less distinct, if present at all, in the cluster of *droogeri* assemblages. With respect to the assemblages of *C. droogeri* most of the *koolhoveni* assemblages have larger mean protoconch-diameters. Only one of the *koolhoveni* samples, from Tjiapoes, plots within the *droogeri* cluster. However, if the mean diameter of protoconch and deuteroconch together is considered instead of the mean protoconch-diameter only, the embryon-size is again larger in this Indonesian assemblage. This is illustrated in the scatter diagram of $\bar{c}_{12}$ versus $\bar{X}$ in figure 16.

In this latter diagram (fig. 16) our sample from Ramla plots well above the other *mediterraneus* assemblages with similar values for $\bar{X}$. This is less distinct in the $\bar{d}_1$-$\bar{X}$ scatter. The data on the Ramla Cycloclypei presented by Drooger (1986) even plot within the cluster constituted by most of the other assemblages of this species. As we have argued earlier, however, our data seem to be more accurate and we therefore maintain that *Cycloclypeus* from Ramla has larger mean embryon-size values than the other *mediterraneus* assemblages with similar $\bar{X}$ values.

In the $\bar{d}_1$-$\bar{X}$ scatter our *eidae* assemblages again constitute a separate cluster together with other assemblages of this species, reported from Indonesia and the Mediterranean. In the $\bar{c}_{12}$-$\bar{X}$ scatter the *eidae* cluster occupies a similar remote position with respect to the assemblages of the other groups.

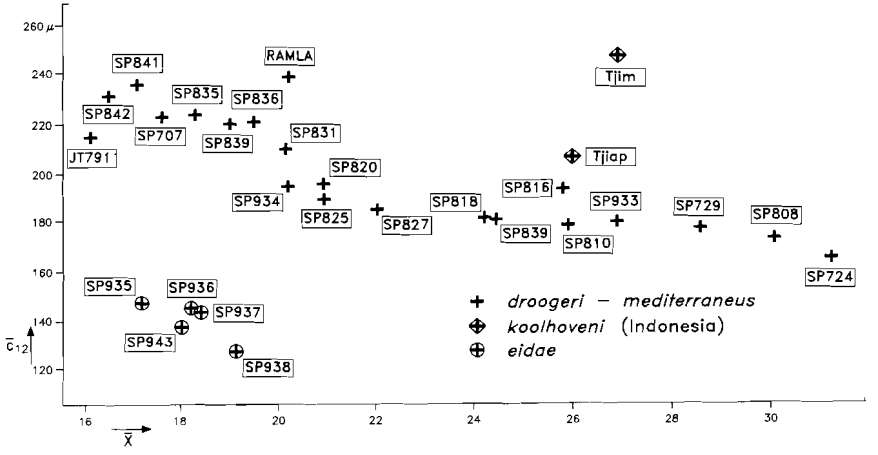

Figure 16: Scatter diagram of mean values of parameters c_{12} and X.

Figure 17 shows the scatter diagram of the mean values of parameters X and γ with separate clusters for *C. droogeri* and *C. mediterraneus*. The morphometric boundary between these species at $\bar{X}$ = 23, would correspond to a

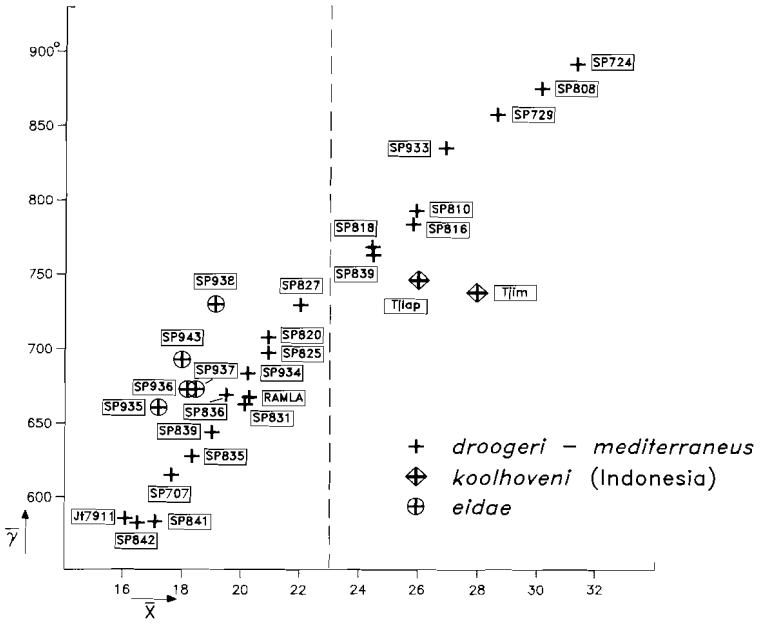

Figure 17: Scatter diagram of mean values of parameters γ and X.

mean value of approximately 750° on the γ-scale. These 23 chambers would thus on average build a precyclic stage of slightly more than two convolutions.

In this diagram our two *koolhoveni* assemblages plot to the right with respect to *droogeri* and *mediterraneus* assemblages with more or less corresponding mean numbers of convolutions. This indicates that the spiral convolutions in *C. koolhoveni* contain more chambers than those in Cycloclypei of the *droogeri* lineage. The *eidae* assemblages, on the contrary, plot to the left of the *mediterraneus* cluster. These Cycloclypei therefore tend to show fewer chambers to a whorl than specimens of the *droogeri* lineage.

IV.2 PARAMETER D_X

In most of our samples the maximum diameter of the nepionic stage, D_X, could be determined in a restricted number of specimens only. Most often this is due to post-mortem damage of the nepionic part of the test. Therefore we selected a number of relatively large and not too badly preserved assemblages: SP707 (*mediterraneus*, Villajoyosa), SP729 (*droogeri*, Villajoyosa; one split only), SP818 (*droogeri*, Lanuza), SP825, SP842 (*mediterraneus*, Lanuza), SP935 (*eidae*, Navazuelo), JT7911 (*mediterraneus*, L'Aquila), IR469 and IR470 (*mediterraneus*,

Ramla). Still, the spiral stages in the more primitive of these assemblages are quite frequently damaged. As a consequence D_X could be measured in less than one third of the Cycloclypei of samples SP729, SP818 and SP825. As large nepionts are more frequently damaged than smaller ones, we expect that the former are less well represented in our observation set than the latter. Therefore the actual mean values of D_X may be somewhat larger than those presented below.

No bimodality was obvious in any of the D_X-distributions of our samples. It should furthermore be mentioned that no systematic differences in D_X were observed for megalospheric and microspheric specimens of the same sample. Yet, the biometric data, which are presented in Table IX pertain to the megalospheric specimens only. In the assemblage of SP935 the D_X values of the *carpenteri*-morphotypes are small but still within the range of variation of those of the group of *eidae*-types. The results for the groups separately would be:

	N	M	SD	SE	V
D_X (mm) *eidae*-types	56	1.08	0.14	0.02	12.6
D_X (mm) *carpenteri*-types	3	0.89	--	--	--

The scatter diagrams in figure 18 contain the observations on *C. mediterraneus* from sample SP707. These diagrams give a general impression of the relations between D_X and the other parameters. The correlation coefficients of these parameter combinations are listed in Table X. In most samples the diameter of the nepionic stage is positively correlated with the number of nepionic chambers and with the number of convolutions. Although, generally speaking, the correlation between γ and D_X seems to be weaker than the one between X and D_X, it is still significant for most samples. It is remarkable that in sample SP729 the r values recorded for both parameter combinations are negative and a significant level ($p = 0.05$) is even reached for the γ-D_X combination. This exceptional result is provisionally ascribed to chance.

As a rule no significant correlations occur between D_X and the parameters measuring the size of the embryon. One significant, negative r value is recorded in sample SP935 for the d_1-D_X combination. However, this correlation may well be false as several different types of Cycloclypei were recognized in this sample. These are indicated by different notations in the two scatter diagrams of figure 19. In the diagram of d_1 versus D_X a main cluster is apparent constituted by the *eidae*-types in the assemblage. The three *carpenteri*-types are easily recognized by their large protoconch dimensions. Finally, the specimen

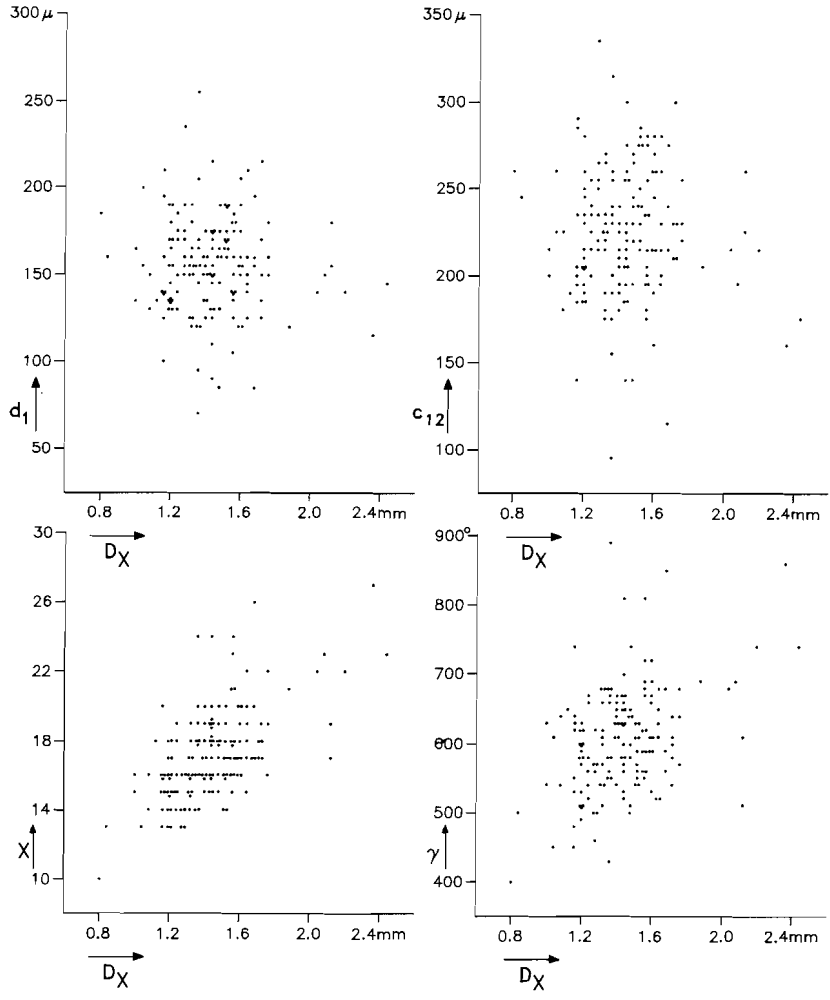

Figure 18: Scatter diagrams of parameter D_X versus parameters d_1, c_{12}, X and γ. Data from sample SP707 (*C. mediterraneus*).

which was provisionally referred to the *droogeri* lineage, plots well away from all other specimens because of its large D_X value. This separation applies to the X - D_X scatter as well, in which this particular specimen again shows a combination of parameter values which is quite unusual regarding the other specimens. Evidently, the specimen would fit in better in an assemblage of the *droogeri* lineage.

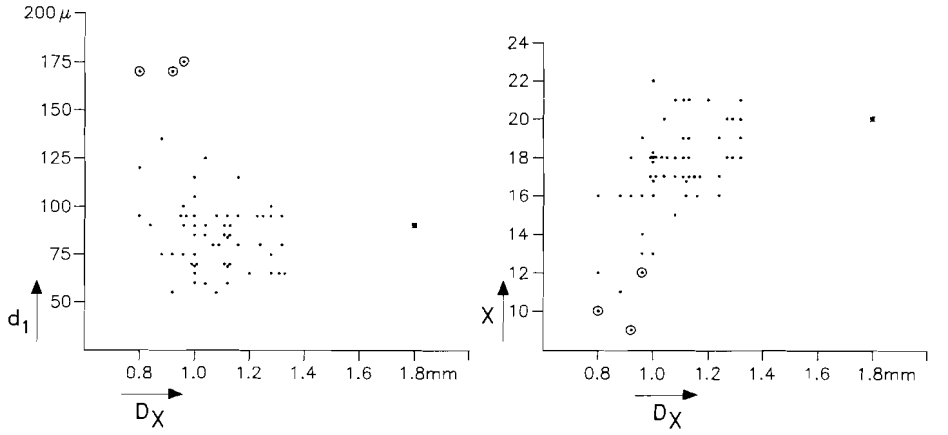

Figure 19: Scatter diagrams of data on the parameter combinations d_1-D_X and X-D_X in SP935 (*C. eidae*). Asterisk refers to presumably reworked specimen; data on the *carpenteri*-types are encircled.

For the group of *eidae*-types in SP935 the correlation coefficients would be:

d_1-D_X	c_{12}-D_X	X-D_X	γ-D_X
r = -0.20	r = -0.14	r = 0.51	r = 0.24
N = 56	N = 56	N = 54	N = 56

All r values are smaller than the earlier ones based on the total number of specimens. The correlation between d_1 and D_X is no longer significant. Although the correlation between γ and D_X is close to the significance level of $p = 0.05$, only the X-D_X combination still shows a distinctly significant correlation ($p < 0.01$).

The positive correlations in our assemblages between parameters X and D_X and between parameters γ and D_X indicate that specimens with a large number of nepionic chambers and a high number of convolutions tend to show a large nepionic stage. This suggests that the size of this stage is to some extent dependent upon the number of nepionic chambers. Somehow, we expected that specimens which started life with a large embryon, would have built a larger nepiont as well. However, a positive correlation between the size parameters of the embryon and the diameter of the nepionic stage is never found. In this context the relations between embryon-size and the nepionic parameters X and γ seem to be of importance. Specimens with large embryons tend to build a small number of precyclic chambers; the ultimate size of the nepionic stage is therefore not necessarily larger in specimens that started life with a large em-

bryon. This view may offer a logical explanation for the correlations between the diameter of the nepiont and the other parameters. But we face a new problem because of the negative correlation between the parameters estimating embryon-size and nepionic configuration, for which no explanation has been offered yet.

Our data seem to suggest that the size of the nepiont is mainly determined by the number of nepionic chambers. However, we can just as well assume the opposite: the number of nepionic chambers being chiefly determined by the ultimate size of the nepiont. In this option the ontogenetic level for the change from spiral to cyclical growth would be size-dependent. The number of growth-steps (cf. X), in which this critical size (cf. D_X) is reached, would furthermore depend upon the size of the embryonic stage: starting from a larger initial size a smaller number of steps would be needed to reach this critical size, i.e. the ultimate size of the nepiont. The well-known but still ill-understood, negative correlation between embryon-size and the number of precyclic

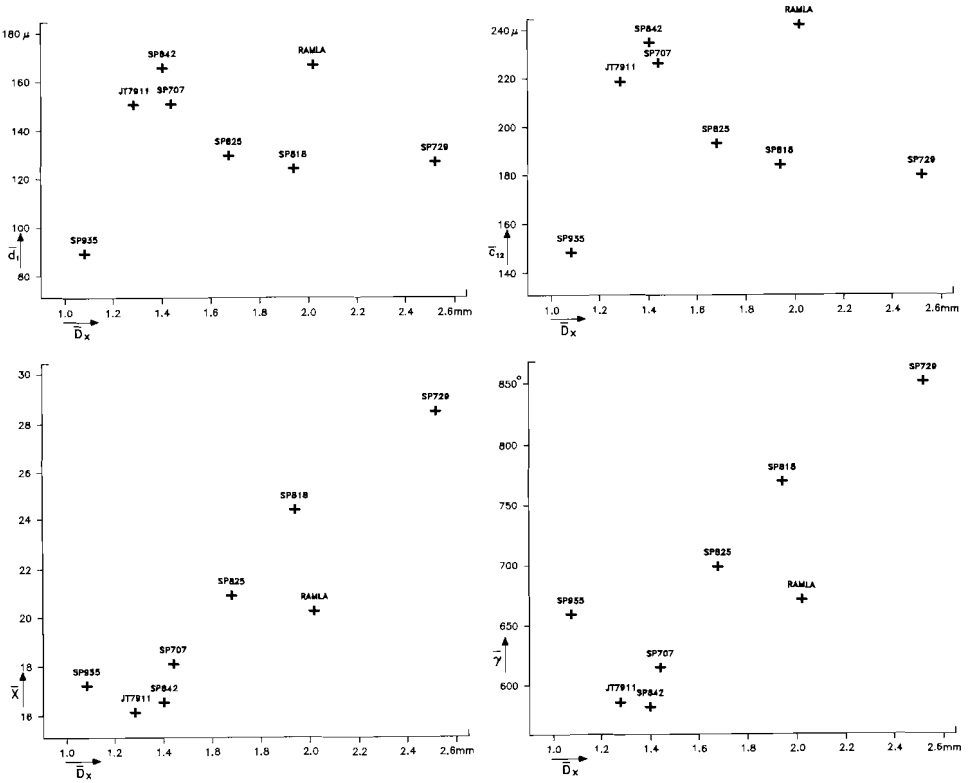

Figure 20: Scatter diagrams of mean values of parameter D_X versus those of parameters d_1, c_{12}, X and γ.

chambers in *Cycloclypeus* can thus be accommodated in this concept. It would simultaneously explain why the nepionic stage in microspheric specimens is built of unusually large numbers of chambers and yet remains comparable in diameter to the nepionic stage of the megalospheric generation.

In the scatter diagrams of figure 20 mean values of D_X are plotted against those of the other parameters. In the diagrams of $\bar{d}_1$-$\bar{D}_X$ and $\bar{c}_{12}$-$\bar{D}_X$ a negative correlation is apparent for the Spanish and Italian assemblages of the *droogeri* lineage. With increasing embryon dimensions a steady decrease is recorded in the size of the nepiont. This decrease in nepionic size, in spite of the overall increase of the initial size of the specimens, is thought to be connected with the concomitant reduction in the number of growth steps in the nepionic stage (cf. X). Mean nepionic size and mean number of nepionic growth steps became reduced in the course of time.

As illustrated by the other two diagrams of the figure, the regressions between $\bar{X}$ and $\bar{D}_X$ and between $\bar{\gamma}$ and $\bar{D}_X$ seem to be almost linear for these samples. The biometric boundary between *C. droogeri* and *C. mediterraneus* ($\bar{X}$ = 23) would correspond to a mean nepionic diameter of approximately 1.9 mm.

In all four diagrams of figure 20 the Ramla sample and the *eidae* assemblage of sample SP935 (including the *carpenteri*-types) become plotted at some distance from the lines of the assemblages discussed above. The Ramla Cycloclypei have larger embryons and smaller numbers of precyclic chambers and of convolutions with respect to assemblages of the *droogeri* lineage with a precyclic stage of similar size. The *eidae* assemblage has a smaller precyclic stage than all other assemblages, including those of the *droogeri* lineage with similar numbers of precyclic chambers and of convolutions. This is consistent with the small embryon dimensions of these Cycloclypei.

Chapter V

RELATIONS BETWEEN EXTERNAL AND INTERNAL MORPHOLOGY

V.1 INTRODUCTION

Several authors considered ornamentation to be of important taxonomic value in *Cycloclypeus*. Brady (1881) distinguished two species among the living representatives of the genus: the ornate *C. carpenteri* and the inornate *C. guembelianus*. Accordingly, Tan (1932) subdivided his *carpenteri* 'sectio' in a *carpenteri* and a *guembelianus* 'subsectio'. Also in the subgenera, which he established for morphotypes with rays and annuli (*Radiocycloclypeus* and *Katacycloclypeus*, respectively), Tan made a subdivision on the basis of the presence or absence of pustules, except for Katacycloclypei with more than one annulus. Cosijn (1938) also distinguished an ornate and an inornate species in his sample from Villajoyosa station (*C.* cf. *carpenteri* and *C.* cf. *guembelianus*, respectively). The concept of two separate lineages existing in the Spanish Oligocene, was subsequently adopted by MacGillavry (1962), who discriminated in addition between an ornate *carpenteri* lineage and an inornate *guembelianus* lineage for Tan's Indonesian data.

Drooger, on the other hand, considered the type of ornamentation to be no more than the expression of ecophenotypic variation in Cycloclypei of a single lineage (Drooger,1955; Drooger & Roelofsen,1982). In the case of Oligocene *Cycloclypeus* from Israel, Laagland (1988) preferred this option to the one advanced by Cosijn and MacGillavry.

Also the distinction of two present-day living species of *Cycloclypeus* has met with serious doubt. A study by Adams and Frame (1979) has shown that the two syntypes of the allegedly inornate *C. guembelianus* are juvenile specimens of which one appeared to be 'ornamented by small irregularly-arranged pustules' while on the second specimen the pustules were reported to be 'numerous and heavy'. As no characteristic internal differences could be observed either, these authors considered *C. guembelianus* to be a junior synonym of *C. carpenteri*.

MacGillavry gave no arguments for the taxonomic importance he ascribed to ornamentation; he merely seems to follow the previous authors Tan and Cosijn. Tan's conclusions are rather difficult to evaluate, however, because of his unusual and rather complicated taxonomical concepts. On page 63 of his monograph he stated for instance (with regard to external morphology):

'Between the representatives of these subsectiones -[*carpenteri* and *guembelianus*]- transitional shapes are not seldom, especially when they occur in the same sample'. On page 120 Tan wrote: 'This lineage -[*C. guembelianus*]- differs from that representing the subsectio of *C. carpenteri* in the sculpture. Similarities are found in the nepionic evolution'. And further on: 'We are of opinion that these subsectiones belong to one and the same lineage'. Finally we quote from page 94: 'The relation between the sculptures of *Radiocycloclypeus stellatus* - [ornate] - and *Radiocycloclypeus radiatus* - [inornate] - is probably the same as that between the sculpture defining the subsectiones *Cycloclypeus carpenteri* and *Cycloclypeus guembelianus*. The specific differentiation is based on this supposition. There is, however, no objection to consider *R. radiatus* as an elementary species - ['mutant' according to p. 97] - of *R. stellatus*'. From this it seems that Tan's data do not warrant a strict separation of ornate and inornate lineages and, moreover, these remarks leave the impression that Tan did not intend such a distinction of autonomous lineages in the first place.

In this chapter we will compare the internal and external morphologies of *Cycloclypeus* individuals in a number of our samples. As these samples derive from mass-transported sediments, their *Cycloclypeus* assemblages probably contain elements from different depth-levels. In this way we will try to investigate the assumption of Drooger and Roelofsen (1982) that the assemblages of the Mediterranean *droogeri* lineage may contain inornate as well as ornate morphotypes and that ornate individuals, which would have lived deeper, have a larger embryon than the inornate specimens from supposedly shallower habitats. Within assemblages of *Cycloclypeus* embryon-size is usually negatively correlated with the nepionic parameters X and γ and therefore these authors expected that nepionic configuration is related to external morphology as well: ornate specimens with their larger embryons would show fewer spiral chambers. This is the more interesting since the differentiation of biometric species like *C. droogeri* and *C. mediterraneus* is based on mean values of X. As a consequence, variation in $\bar{X}$ due to environmental conditions might interfere with the biostratigraphic value assigned to these species by Drooger and Laagland (1986).

V.2 EXTERNAL MORPHOLOGY

The well preserved *Cycloclypeus* assemblages from Ramla will serve to illustrate the external features generally encountered in the *droogeri* lineage. The central part of the disc-shaped test is usually thickened and may be pinnacle-like to broadly dome-shaped. The thickness of the surrounding flange tends to increase as more chambers are added but it shows only little variation in large

specimens. The surface of the test may furthermore be provided with various sculptural elements.

Frequently an ontogenetic zonation in types of ornamentation can be observed in single specimens (plate 1, fig. 3; plate 2, fig. 1). The youngest chambers may be smooth, whereas the next older ones may show raised sutures over the septula between the chamberlets. In still older parts of the test these raised sutures may have developed a more prominent distal part occupying a larger area, which gives the ornaments a drop-like appearance. In the central part of the test this kind of lateral expansion may bring about blunt and broadly rounded pustules. As in small, juvenile forms a well developed ornamentation consists of no more than raised sutures, the recorded zonation probably results from a differential lamellar thickening of the walls during the life-time of the organism.

Not all types of ornamentation are necessarily present in sculptured adult specimens. Ornamentation may consist essentially of raised sutures or of blunt to drop-like pustules only. Furthermore, lateral expansion of the ornaments is absent in some rare specimens covered by sharply bound, thin pustules (plate 1, fig. 5). Occasionally, raised sutures split into two pustules: one as usual at the junction of septulum and frontal septum and the other in a more proximal position (plate 2, fig. 2). Finally, pustules may fuse laterally into ridges, overlying the septa (plate 1, fig. 4). As far as could be ascertained, no sculptural elements are present on the chamberlet walls proper.

The height of the ornaments is variable and a gradation is present to smooth individuals. No interrelation is observed between height and type of ornamentation. The sculptural elements are often marked by differences in colour; they may be milky-white to glassy in contrast to the usually yellowish colour of the rest of the wall. This difference is usually more conspicuous in specimens with a high sculptural relief. No interrelation is apparent between the height of the sculpture and the thickness of the test.

In general, this description of the Ramla specimens is characteristic for the entire *droogeri* lineage but some particular deviations have been observed. Compared to most of our other assemblages, ornate specimens are more frequent at Ramla. Moreover, at this locality the range of variation extends to morphotypes with an exceptionally high sculptural relief. In addition, specimens covered by sharply bound, thin pustules, in which lateral expansion of the ornaments is lacking (rare at Ramla), were not observed in the other samples. Finally, in some of the European samples (e.g. SP729) the central swelling tends to be larger and thicker in inornate specimens, which tend to be thicker over the flange as well.

Although the sculptural design described so far is essentially the same in the

younger *C. eidae* from Spain, the external appearance of these specimens is conspicuously different (plate 3, figs. 1-3). In contrast to the ornamentation in the *droogeri* lineage, the sculptural elements show but little lateral expansion and the specimens are easily recognized by their delicate, closely set pustules. Often the older and younger parts of the test are equally ornamented with such fine pustules, except for the youngest, peripheral part, which may show raised sutures grading into drop-like pustules. Furthermore the central swelling of the test is often less pronounced in *C. eidae* and covers a smaller area than in representatives of the *droogeri* lineage.

Tan (1932) described the ornamentation of Indonesian *Cycloclypeus* in general terms only, but inspection of his plates reveals more specific information. In the case of *C. koolhoveni* these additional observations could be corroborated by a study on material from Tjimanggoe, which is the type-locality of the species (Kesseler,int.report). The sculptural design in the *koolhoveni* lineage does not differ fundamentally from that observed in the older species of the Mediterranean realm. As a rule ornaments have not expanded laterally, which trait seems to be characteristic for the *droogeri* lineage (plate 4, figs. 1, 2). The fine pustules which cover the Indonesian specimens appear to be more numerous, as raised sutures more frequently split into two or more pustules and occasional pustules are located on the chamberlet walls as well.

No differences in external appearance could be discerned between the Indonesian and the Mediterranean *eidae* assemblages.

In our material specimens from a selected number of samples have been grouped into three classes according to the height of their sculptural relief. Badly damaged as well as juvenile specimens were discarded. The samples derive from three Spanish localities (SP707,SP710,SP729), from the Italian L'Aquila locality (JT7911) and from the Ramla locality in Israel (IR469,IR470). During the subsequent biometric study of the internal features, the annotations on external morphology were kept apart to minimize bias.

As no breaks are apparent in the range of sculptural variation, the boundaries between the classes are arbitrary. Individual specimens may be difficult to label but the resulting groups are on the average distinctly different in external appearance. They were defined (Laagland,1988) as follows:

- Group A ('inornate') : Specimens with a smooth to very weakly sculptured test (plate 1, fig. 1).
- Group B ('intermediate') : Specimens showing a weak to modest sculpture, which is often distributed in patches on the test (plate 1, figs. 2, 3; plate 2, fig. 1).

- Group C ('ornate') : Specimens showing a well to highly developed sculpture (plate 1, figs. 4, 5; plate 2, fig. 2).

Partial mean parameter values and related statistics were calculated for the separate morphogroups which procedure enables us to compare the three groups within each assemblage. However, in comparing the biometrical results on these groups from one assemblage to the other we are not so much interested in the actual, numerical value of a parameter mean within a group but rather in its difference from the grand mean of the total assemblage from which it stems. Therefore we converted the distributions, based on the total number of observations within each sample, having a mean value of M_{tot} and a standard deviation of SD_{tot}, to another distribution with the mean value at 0.0 and the SD_{tot} as scale unit. This is done by converting each score into its distance from the grand mean (M_{tot}), which distance is expressed in fractions of the standard deviation of the entire sample (SD_{tot}):

$$Score_{standard} = \frac{Score_{observed} - M_{tot}}{SD_{tot}}$$

Of course the statistics for each group calculated from these standardized scores can also be obtained from the statistics based on the original data set:

$$\text{Standardized } M_{part} = \frac{M_{part} - M_{tot}}{SD_{tot}}$$

$$\text{Standardized } SD_{part} = \frac{SD_{part}}{SD_{tot}}$$

$$\text{Standardized } SE_{part} = \frac{SE_{part}}{SD_{tot}}$$

Provided that distributions are sufficiently similar, this procedure has the advantage that we can compare partial means of different samples, regardless of the actual values of the total means.

Another important implication of this procedure is the possibility to lump the standardized data sets of several samples when the numbers of observations in the single samples are low. The samples from the Spanish Lanuza section were thus arranged into two groups, which were labelled Lanuza-1 and Lanuza-2. Lanuza-1 is constituted by the lower four samples, containing the *droogeri*

assemblages (SP808,SP810,SP816,SP818) and Lanuza-2 by the remaining, *mediterraneus* assemblages (SP820,SP825,SP827,SP831,SP835,SP836,SP839, SP841,SP842). The statistical results on such lump-samples are presented in the standardized format only; for single samples the results are given in both real and standardized values.

V.3 EMBRYON-SIZE AND NEPIONIC CONFIGURATION

In this subchapter the data are presented on the parameters which estimate the size of the embryonic chambers and the configuration of the nepionic stage: d_1, c_{12}, X and γ. As in the previous chapter the biometric data on parameter D_X are presented separately.

V.3.1 Villajoyosa

Exposure 4 of Cosijn (1938), situated opposite the station of Villajoyosa, was resampled (SP710). Our *Cycloclypeus* assemblage contained 23 'inornate' specimens (group A), 30 'intermediate' specimens (B) and 4 'ornate' specimens (C). Six specimens could not be allocated to one of the three groups as they were too badly preserved or too small.

The two lowermost distributions in figure 21 pertain to the total numbers of observations on X in our sample and in the sample of Cosijn. Our sample is represented by 54 observations only, as parameter X could not be determined in all of our specimens. The distributions show a close resemblance and in both a peculiar long tail is observed, representing specimens with a large number of precyclic chambers. Accordingly, relatively large values for the coefficient of variability are recorded (V_X: 26.7 and 19.8 in SP710 and in Cosijn's sample, respectively). The difference between the mean values of X is smaller than one standard error and therefore not significant.

A more complex picture arises from the comparison of the X-distributions within each of the groups distinguished on external morphology. To this end we compared Cosijn's smooth *C.* cf. *guembelianus* with our inornate group A and his ornamented specimens of *C.* cf. *carpenteri* with our specimens in the intermediate group B and in the rather small ornate group C together.

The relevant distributions in figure 21 clearly show the overall larger X-values in *C.* cf. *guembelianus* with respect to *C.* cf. *carpenteri* in the observations of Cosijn. No such difference is apparent, however, in the distributions of our SP710 groups. Our group, thought to correspond to *C.* cf. *carpenteri*, also shows relatively large numbers of specimens with low X-values but in addition there are several specimens with X-values of 25 and higher. In fact, this distribu-

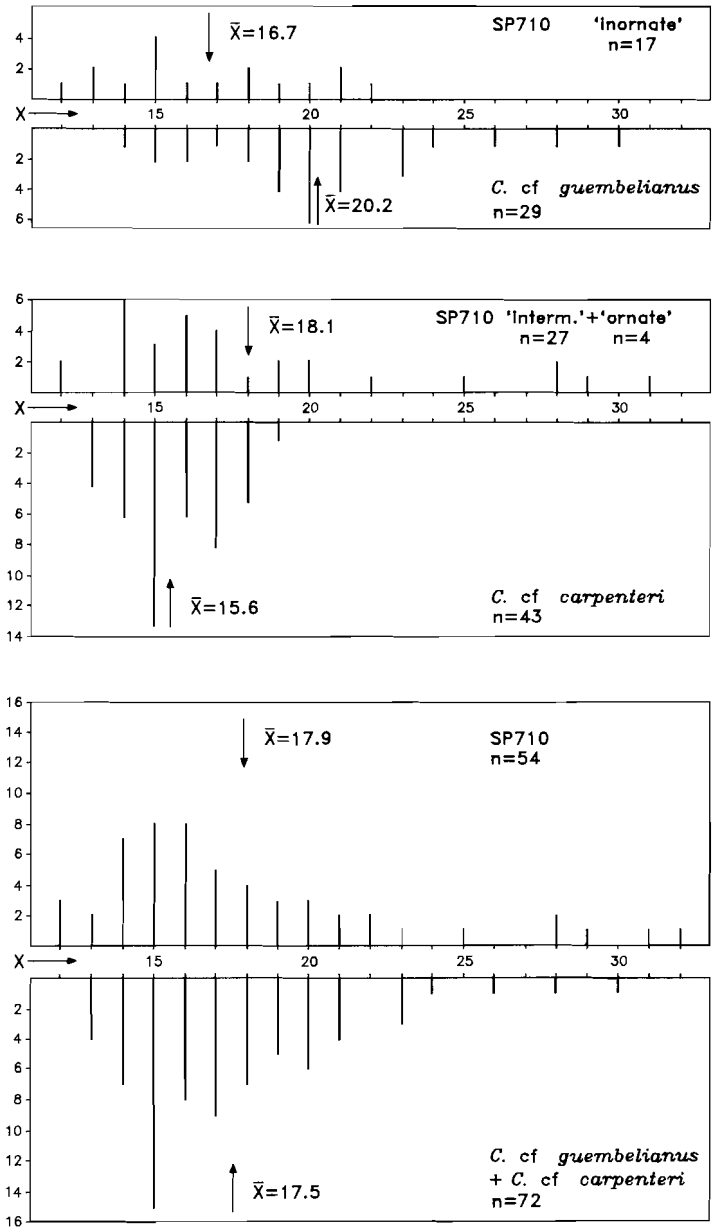

Figure 21: Frequency distributions of parameter X in our sample SP710 and in Cosijn's sample from Villajoyosa station.

tional tail in our ornamented lump-group seems to correspond to the tail in Cosijn's smooth *C.* cf. *guembelianus*, whereas such a high-value array is absent in the X-distribution of our inornate group.

There is a significant difference in the mean X values of *C.* cf. *guembelianus* and our inornate group at the level of $p=0.01$, and at the same level of probability a difference exists in $\bar{X}$ for *C.* cf. *carpenteri* and our ornamented lump-group. In *C.* cf. *guembelianus* the number of precyclic chambers is significantly larger than in *C.* cf. *carpenteri*, whereas for our two groups differences in all four parameters employed are not significant.

Summarizing, we conclude that our data on the internal morphology of the Cycloclypei from the Villajoyosa locality are not compatible with those presented by Cosijn (1938), when distinction is made between groups based on external morphology.

Both samples derive from the same locality and both show the same remarkable type of X-distribution if the total numbers of observations are considered. In this respect there is little support for the assumption that these samples represent two different populations. It seems equally difficult to attribute the large discrepancy in the results of both studies to differences in the delimitation of the morphogroups distinguished on external morphology. The criteria employed are quite straightforward and there is a fair correspondence between the ratios of these groups in both samples.

However, Cosijn reports that after he had sectioned the larger part of his specimens he started to suspect heterogeneity in the sample on account of the unusual shape of the X-distribution. Closer inspection of the remaining specimens revealed the variation in ornamentation and only then he split the remaining material in a 'smooth' and a 'pillared' group. For these two groups of remaining specimens differences in the ranges of X and d_1 were observed. In spite of the fact that these ranges showed large overlaps, Cosijn concluded: 'As of the originally examined sample the number of heterosteginoidal septa - [cf. X]- . . . was known of each specimen, it was still possible to trace which specimens must have been pillared and which must have had smooth shells'.

In this conclusion we do not agree with Cosijn. It is not realistic to allocate sectioned specimens to one of the external morphogroups if these groups are previously reported to show large overlap in their internal characters. We therefore consider Cosijn's procedure, on which he based the distinction of an inornate and an ornate *Cycloclypeus* lineage in the Spanish Oligocene, to be invalid.

In the scatter diagram of our data on d_1 and X (fig. 22) a main cluster is apparent, in addition to a small number of more remote specimens with large X-

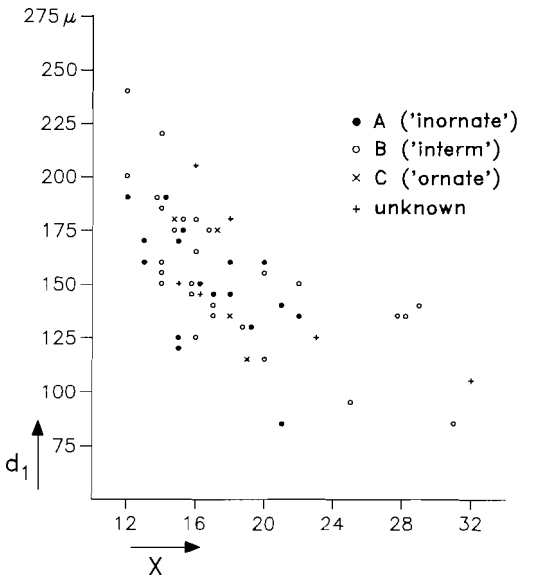

Figure 22: Scatter-diagram of d_1 versus X in SP710 with data on ornamentation.

values. This indicates that the Villajoyosa assemblage may well be heterogeneous in composition but it is doubtful whether this heterogeneity corresponds to the observed variation in ornamentation. Cosijn states that he observed the pillared morphotypes in the sample from Villajoyosa station only, where they occur in combination with the more common smooth types. But our material shows that several assemblages from the region contain a mixture of ornate and inornate specimens and, in general, no such broad variation in internal features is present in these samples. Moreover, most of our Villajoyosa specimens with 'conservative' internal characteristics are ornamented (type B), whereas the corresponding specimens in Cosijn's sample were considered to be smooth.

In this region, with its tectonic activity during Oligocene time, reworking from older strata may easily have led to the admixture of more primitive *Cycloclypeus* in the mass-transported sediments. Cosijn considered this possibility as well but he rejected it because he did not find supporting evidence in the other constituents of the Villajoyosa association. This accompanying fauna, however, does not contain rapidly evolving groups like *Cycloclypeus*, in which reworking could be easily recognized. So we are inclined to accept the alternative explanation of reworking which means that our Villajoyosa sample is not suitable to investigate the hypothesis of Drooger and Roelofsen (1982). For

this we evidently need samples that contain individuals deriving from different but more or less contemporaneous depth-assemblages.

V.3.2 Other European samples

The three morphogroups A, B and C were distinguished in five other European samples. *C. droogeri* is present in sample SP729 and the Lanuza-1 lump-sample and *C. mediterraneus* in SP707, JT7911 and Lanuza-2. From the frequency curves and scatter diagrams of the biometric data no heterogeneity is apparent in any of these samples, as was already noted in the previous chapter. Therefore the specimens from each sample (or from each assemblage pertaining to our lump-samples) are thought to derive from a restricted time-interval, while no separate ornate and inornate species and lineages can be distinguished within these samples.

Univarate analysis

For samples SP729, SP707 and JT7911 mean parameter values and associated statistics of the single morphogroups are presented in Table XI. Values in Table XII, representing similar information, result from calculations on the standardized data sets of all five samples. In figure 23 the partial mean parameter values ($\pm$ 1 SE) are presented graphically. This figure shows that embryon-size tends to be larger in the more ornamented groups but in none of the samples differences reach significant values. On the other hand the figure indicates that the values of the nepionic parameters X and γ are generally larger in the least ornamented group. In the Lanuza-2 lump-sample these differences are large enough to be significant. The results from Student's t-tests are listed below.

Lanuza-2 $\bar{X}$:	$t_{A-C} = 2.45$	$df = 41$	$p < 0.02$
	$t_{B-C} = 3.11$	$df = 134$	$p < 0.01$
$\bar{\gamma}$:	$t_{A-C} = 2.16$	$df = 44$	$p < 0.05$
	$t_{B-C} = 2.26$	$df = 142$	$p < 0.05$

In sample SP729 differences are close to significance. However, if the intermediate and ornate groups are lumped, the difference in $\bar{X}$ for this lumped group and the inornate A group is significant at the level of $p = 0.05$.

SP729 $\bar{X}$:	$t_{A-B} = 1.74$	$df = 119$	$p < 0.1$
	$t_{A-C} = 1.93$	$df = 60$	$p < 0.1$
	$t_{A-BC} = 2.02$	$df = 131$	$p < 0.05$
$\bar{\gamma}$:	$t_{A-B} = 1.81$	$df = 122$	$p < 0.1$

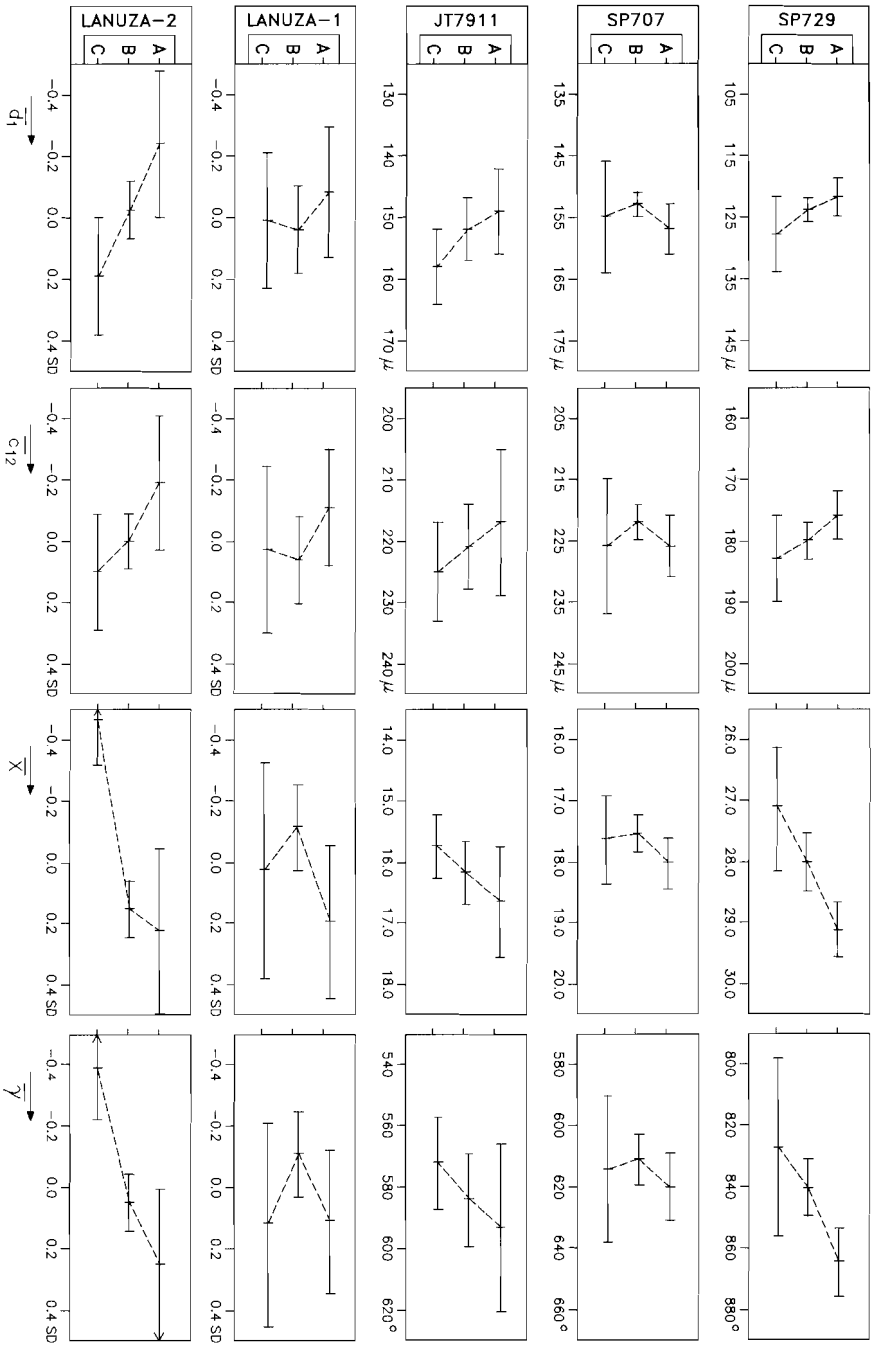

Figure 23: Partial mean parameter values (± 1 SE) of the morphogroups in the European samples. Lump-sample values are presented in standardized version.

Frequency distributions and scatter diagrams of both samples are reproduced in figures 24 to 26 (Lanuza-2) and figures 27 to 29 (SP729). These figures show that without statistical analysis differences are of doubtful character.

Partial mean values of c_{12} and X, calculated from the standardized data sets of the five (group-)samples, have been entered in figure 30. The intermediate groups cluster near the centre of the figure, which point represents the mean of the total number of observations on c_{12} and X for each sample. Most of the

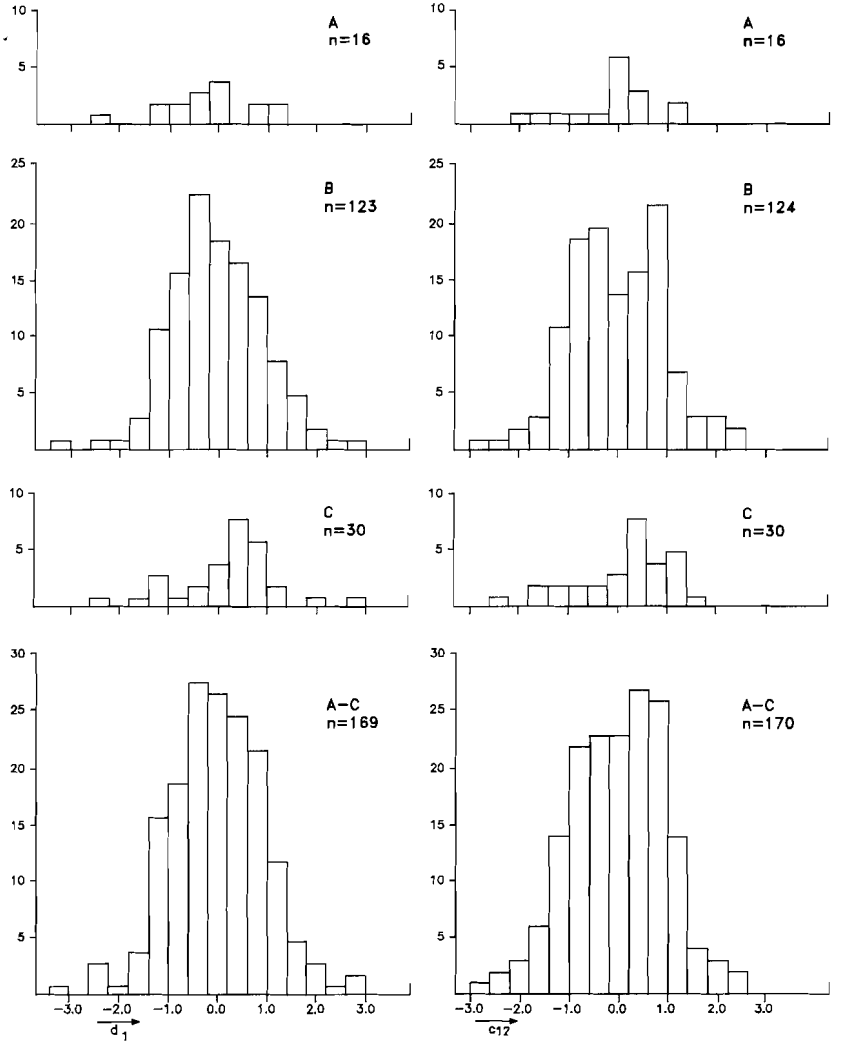

Figure 24: Frequency distributions of standardized data on d_1 and c_{12} in Lanuza-2 (*C. mediterraneus*).

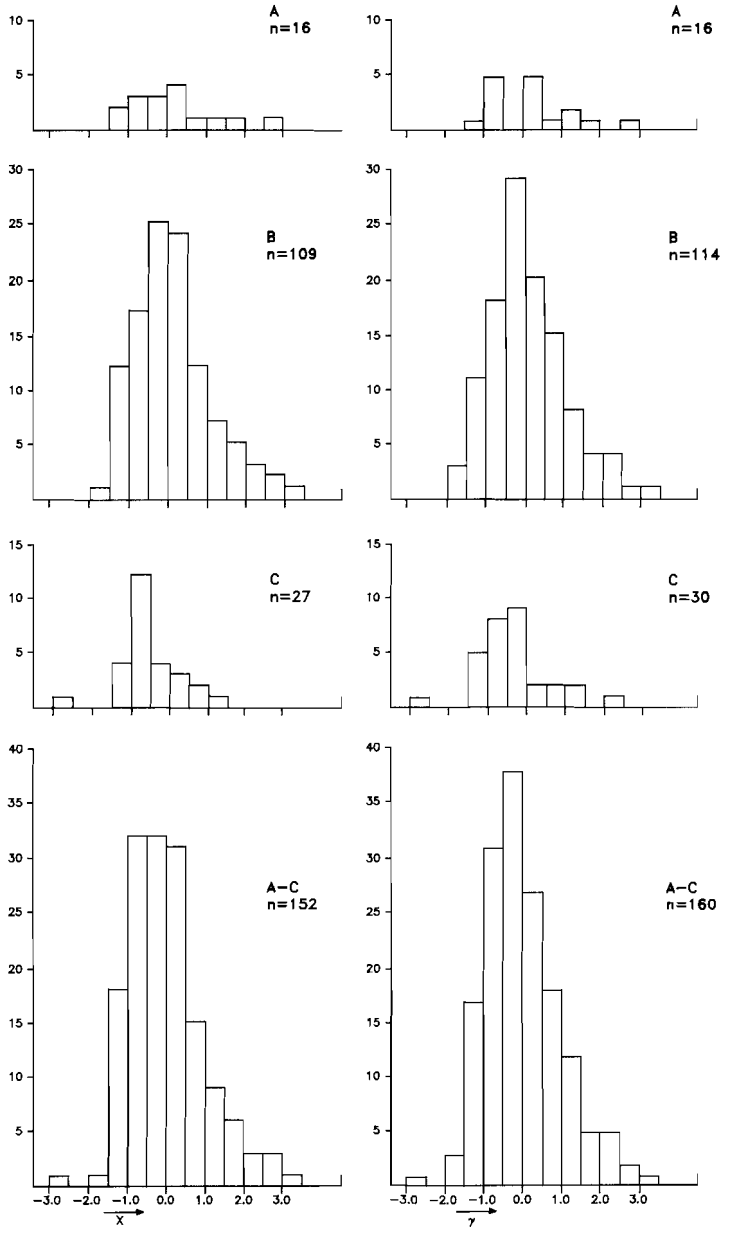

Figure 25: Frequency distributions of standardized data on X and γ in Lanuza-2 (*C. mediterraneus*).

inornate groups are situated in the 'smaller embryon - larger X' part of the diagram. The points of the ornate groups show overlap with the intermediate group and extend towards the 'larger embryon - smaller X' part of the diagram. From this figure it is apparent that the variation in the standardized mean values of X is larger than the one in standardized mean embryon-size values.

Finally we lumped all standardized observations available and again calculated mean values for the three morphogroups. The results are summarized in Table XIII and figure 31. Still there are no significant differences in the embryon-size parameters ($p > 0.1$), whereas a number of significant, or nearly significant differences occur in the nepionic parameters, which are most distinct in the $\bar{X}$-values.

All data $\bar{X}$:	t_{A-B} = 2.01	df = 499	$p < 0.05$
	t_{A-C} = 3.15	df = 247	$p < 0.01$
	t_{B-C} = 1.97	df = 438	$p < 0.05$
$\bar{\gamma}$:	t_{A-B} = 1.80	df = 521	$p < 0.1$
	t_{A-C} = 2.34	df = 261	$p < 0.05$

We conclude that in assemblages of *C. droogeri* and *C. mediterraneus* from the European Oligocene a relation is present between external and internal morphology. Ornate morphotypes tend to have fewer precyclic chambers than specimens with an intermediate external morphology, which in turn tend to show fewer precyclic chambers than the inornate morphotypes. Furthermore,

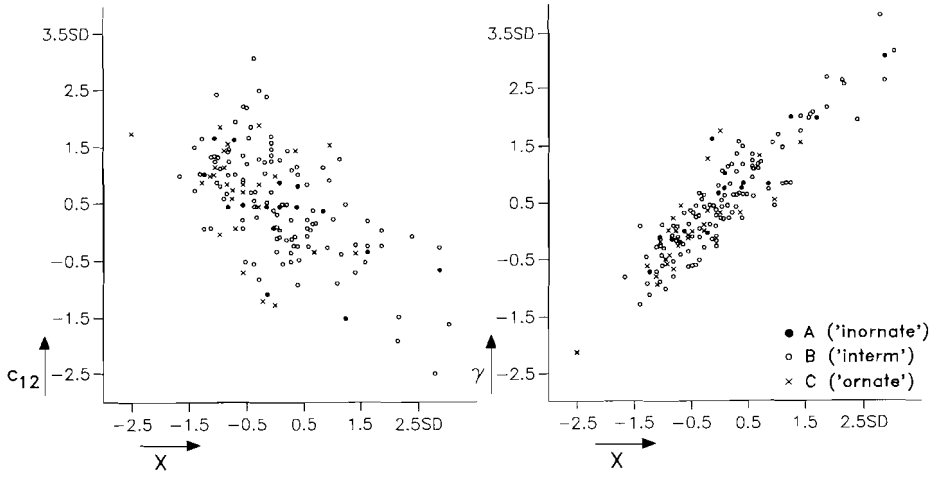

Figure 26: Scatter diagrams of standardized data on parameter pairs c_{12}-X and γ-X in Lanuza-2 (*C. mediterraneus*).

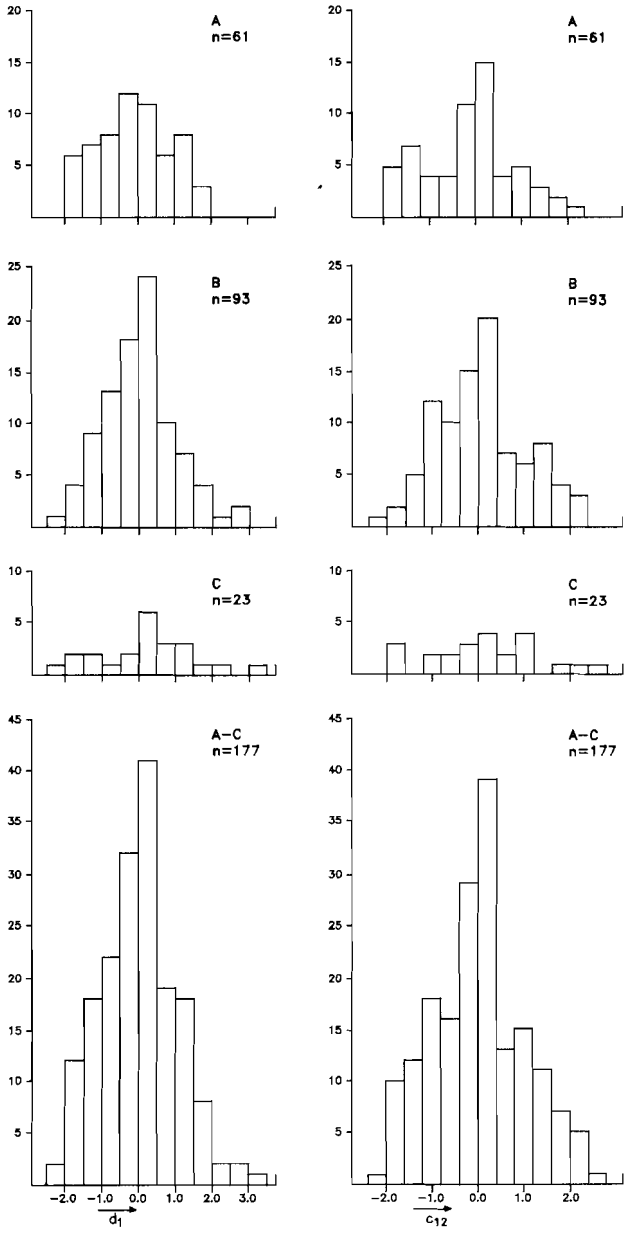

Figure 27: Frequency distributions of standardized data on d_1 and c_{12} in SP729 (*C. droogeri*).

the number of convolutions in the nepionic stage is generally smaller in ornate specimens than in inornate ones. This difference in γ is, however, less significant than the difference in X. The size of the embryon generally tends to be larger in more ornamented specimens but the recorded differences are too small to be of statistical significance.

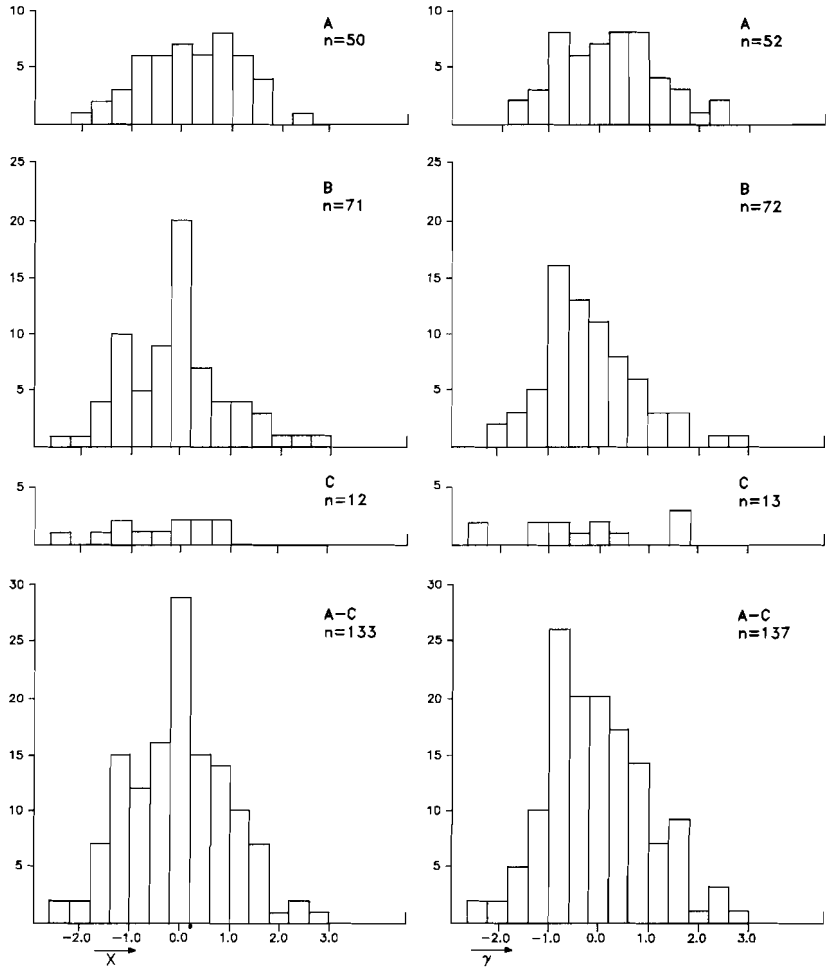

Figure 28: Frequency distributions of standardized data on X and γ in SP729 (*C. droogeri*).

Bivariate analysis

The negative correlation between embryon-size and nepionic configuration which is usually recorded within the assemblages of *Cycloclypeus*, was already

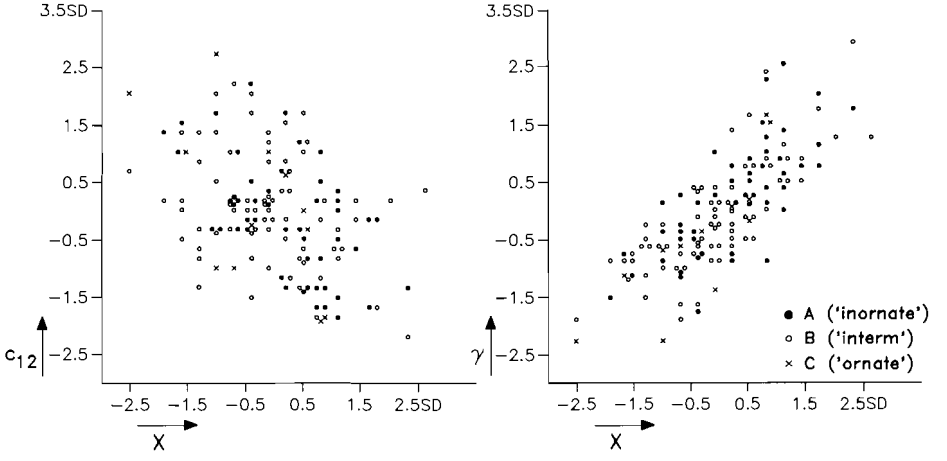

Figure 29: Scatter diagrams of standardized data on parameter pairs c_{12}-X and γ-X in SP729 (*C. droogeri*).

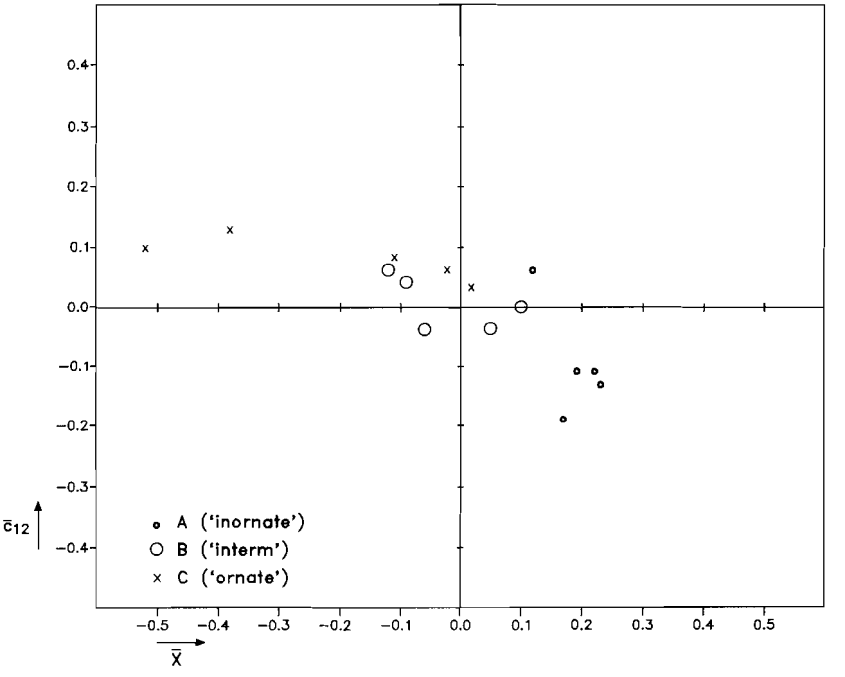

Figure 30: Scatter diagram of standardized mean values of parameters c_{12} and X of the morphogroups in the European samples.

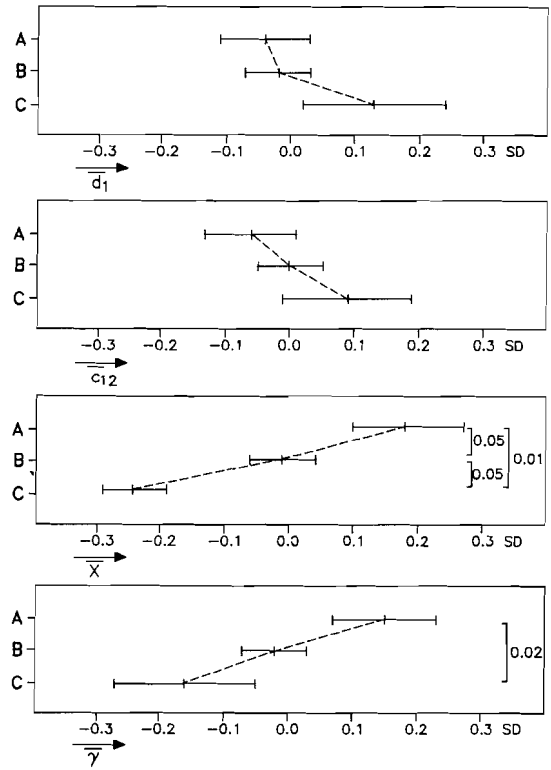

Figure 31: Standardized mean parameter values (± 1 SE) of the morphogroups in the five European samples together. Significance levels of differences are indicated.

discussed in the previous chapter. As might be expected the differences in partial mean values for the morphogroups of all four parameters tend to show a similar relation (fig. 31). More ornate groups, having overall larger embryons, have smaller mean numbers of precyclic chambers and of convolutions. However, the data leave the impression that the differences in the embryonic parameters are disproportionately small relative to the corresponding differences in the nepionic ones. This might indicate that in addition to the differences in the single characters also the relations between these characters differ in the three morphogroups.

To check whether this notion could be substantiated, we first of all calculated the values of correlation coefficients within the morphogroups for comparison with those based on the observations of all three groups together. We arbitrarily chose d_1 to represent the embryon-size parameters. r values of the resulting parameter combinations d_1-X and d_1-γ are listed in Table XIV and are graphically presented in the scatter diagram of figure 32.

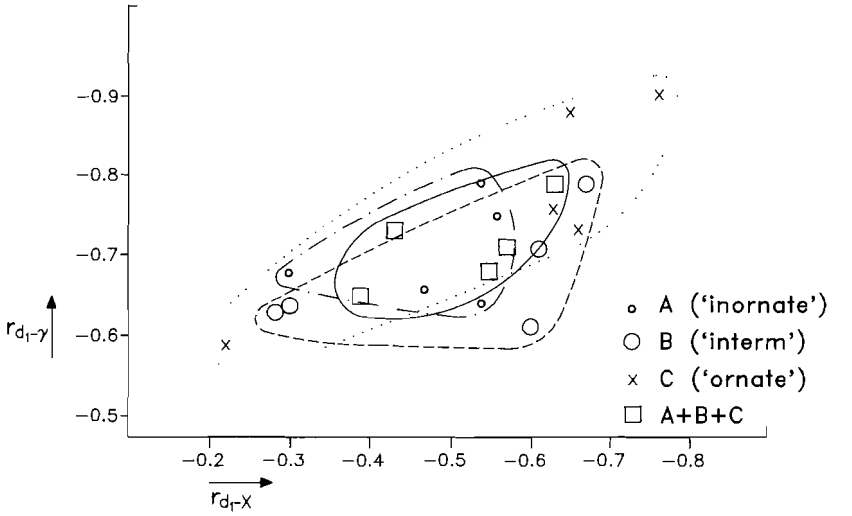

Figure 32: Scatter diagram of the partial correlation coefficients in the three morphogroups and in the total data set for the parameter combinations d_1-X and d_1-γ; European samples only.

This figure shows that the partial r values of single morphogroups vary considerably from sample to sample. However, only one cluster is apparent. The data on groups A and B are evenly distributed over this cluster in which the data on the lump-category A-C (A+B+C) occupy a more central position. The r values in group C tend to reach smaller than usual, negative values but one sample of this group occupies the other extreme end of the cluster. We have to bear in mind that a number of values are based on rather small samples. Therefore it cannot be proved that they are significantly different from those in the other categories. If we increase the number of observations by lumping the data sets of all five of our European samples, the smallest negative r values are again reached in the ornate groups of specimens. But the variation in the values of all categories is small; for the d_1-X combination values range from -0.52 to -0.59 and for the d_1-γ combination from -0.70 to -0.78. Therefore the correlation-coefficients for the respective parameter combinations are considered to be similar in all three morphogroups distinguished.

A second approach seems to be available to reveal whether the relations between the parameters are really different in the three morphogroups. We could check to what extent the observations of single morphogroups are evenly distributed over the clusters in the scatter diagrams of our samples. Actually, these clusters show large overlap and, if such differences are present at all, they are expected to be small, while large numbers of data will be needed to detect

them. This condition can best be met by lumping the data sets of our five European samples. However, to keep the resulting information surveyable, it has to be condensed in some way. This has been done by splitting each cluster of observations into smaller portions, which are subsequently represented by their bivariate mean values of the separate morphogroups. The parameter combinations c_{12}-X and c_{12}-γ were studied in this way and the specimens of each morphogroup were arranged in classes according to their scores on the embryon-size parameter. The interval of $-2.5\ SD_{tot} < \bar{c}_{12} < +2.5\ SD_{tot}$ was split in portions of one SD_{tot}. As this is also the scale-unit in which the standardized scores are expressed, the range of these portions is exactly 1.0. The results of this procedure are presented in the two diagrams of figure 33.

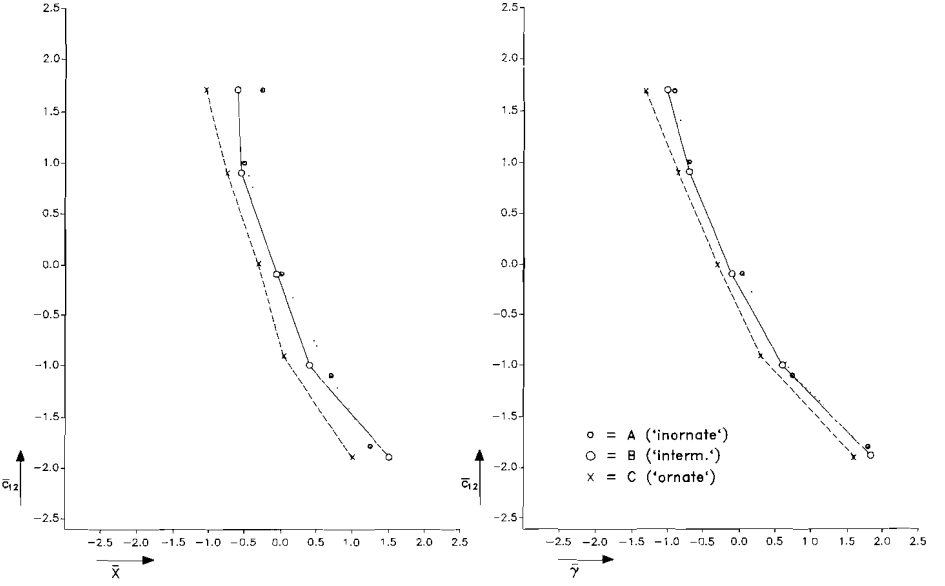

Figure 33: Plots of the bivariate mean values of the parameter combinations c_{12}-X and c_{12}-γ for successive c_{12} intervals of the standardized European data set. Boundaries coincide with the values of -2.5, -1.5, -0.5, +0.5, +1.5 and +2.5 on the c_{12} scale.

In both diagrams the bivariate means representing the observations on the ornate specimens are observed to plot to the left of the corresponding points representing the other two morphotypes. Additionally, nearly all of the bivariate means of the intermediate group occupy a similar position with respect to means of the inornate group of specimens. This pattern suggests that at every embryon-size level, more ornamented specimens tend to show fewer precyclic chambers and fewer convolutions.

If, on the other hand, one would wish to consider the pattern as merely due

to chance, the relation between embryon-size and nepionic configuration would on average be the same in all morphogroups. In the latter case the bivariate mean of one morphogroup has an equal chance to become plotted to the left or to the right of the corresponding point representing the next morphogroup, if we consider the chance for identical mean values to be practically zero.

The chance that all five points of the ornate group are positioned to the left of the corresponding points of the intermediate group -as they actually are- will be 1:32 ($0.01 < p < 0.05$). Simultaneously, however, the same relation is observed between the points of the ornate and inornate groups, respectively,

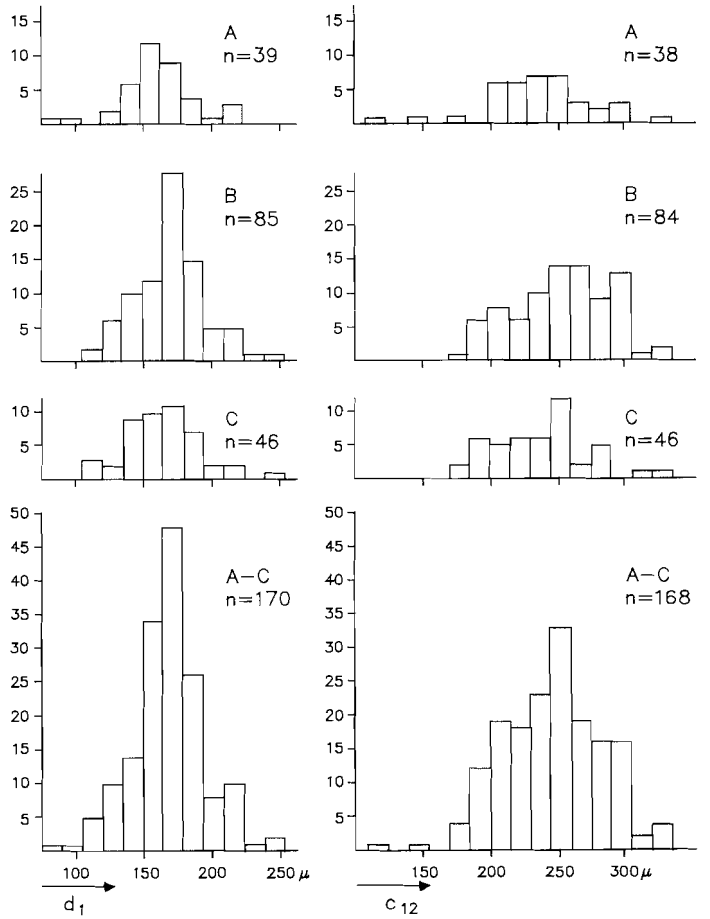

Figure 34: Frequency distributions of d_1 and c_{12} in IR469 (*C. mediterraneus*).

which further reduces the probability that our results are due to chance to 1:1024 ($p < 0.001$).

We therefore think that it is safe to conclude that the average relation between embryonic and nepionic parameters is not identical for the three morphogroups. At any embryon-size level the number of precyclic chambers is generally smaller in more ornamented specimens. This is most distinct for the ornate group of specimens with respect to the other morphotypes. Regarding the number of convolutions, γ, a similar picture arises although the differences between the morphotypes appear to be less distinct.

Our morphological study of the European Cycloclypei largely confirms the hypothesis of Drooger and Roelofsen (1982). These authors expected, however, that differences in nepionic configuration, linked to external morphology, would result from variation in embryon-size. This hypothesis can not be substantiated. Differences in the mean embryon-size of the three morphotypes appear to be of low significance, whereas variation in the nepionic configuration is much larger and cannot be merely explained by differences in embryon-size.

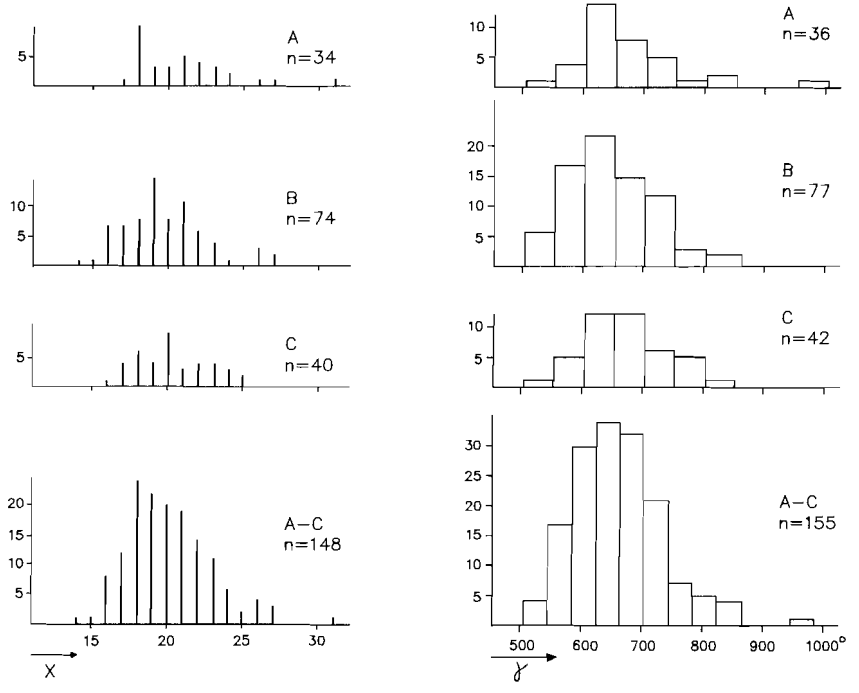

Figure 35: Frequency distributions of X and γ in IR469 (*C. mediterraneus*).

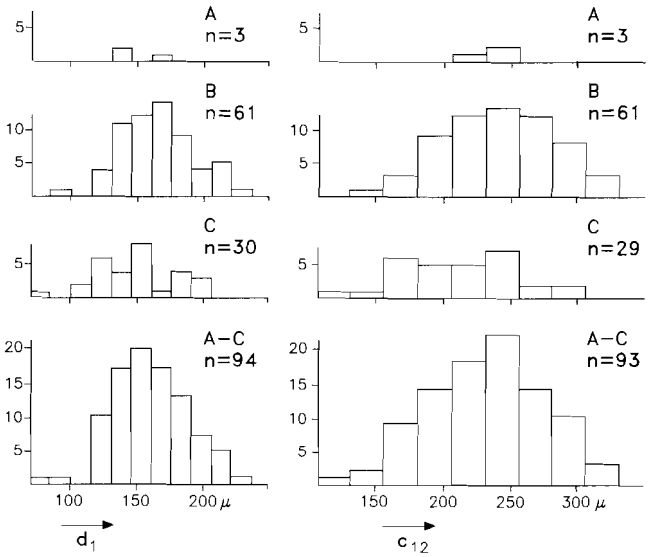

Figure 36: Frequency distributions of d_1 and c_{12} in IR470 (*C. mediterraneus*).

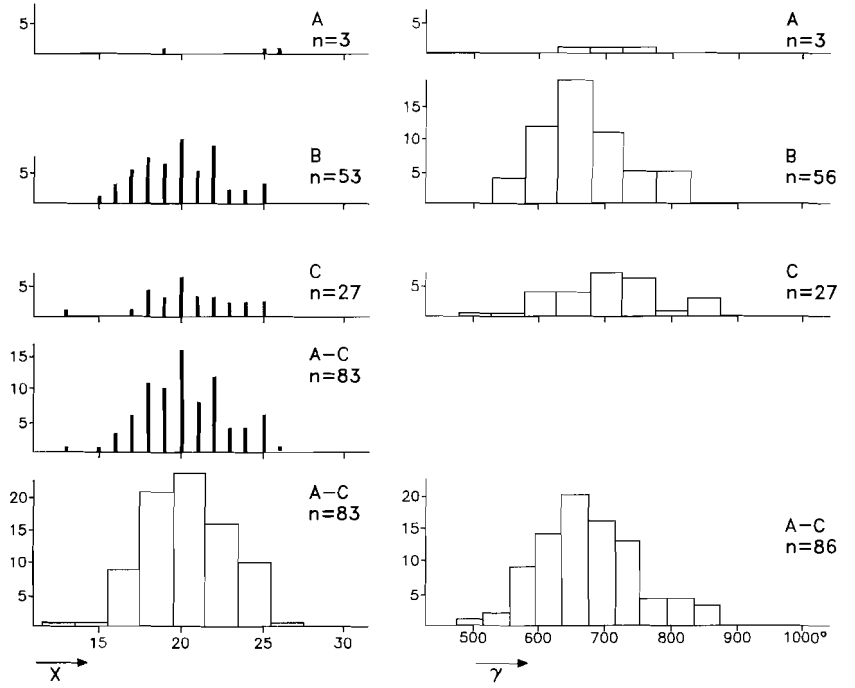

Figure 37: Frequency distributions of X and γ in IR470 (*C. mediterraneus*).

V.3.3 Israel

Data on the Ramla sample IR469 from Israel were published in an earlier paper (Laagland,1988) and are reproduced here together with those on sample IR470 from the same locality. This second sample contains but a few inornate individuals. Frequency distributions are presented in figures 34 and 35 (IR469), 36 and 37 (IR470) and scatter diagrams in figures 38 (IR469) and 39 (IR470). As

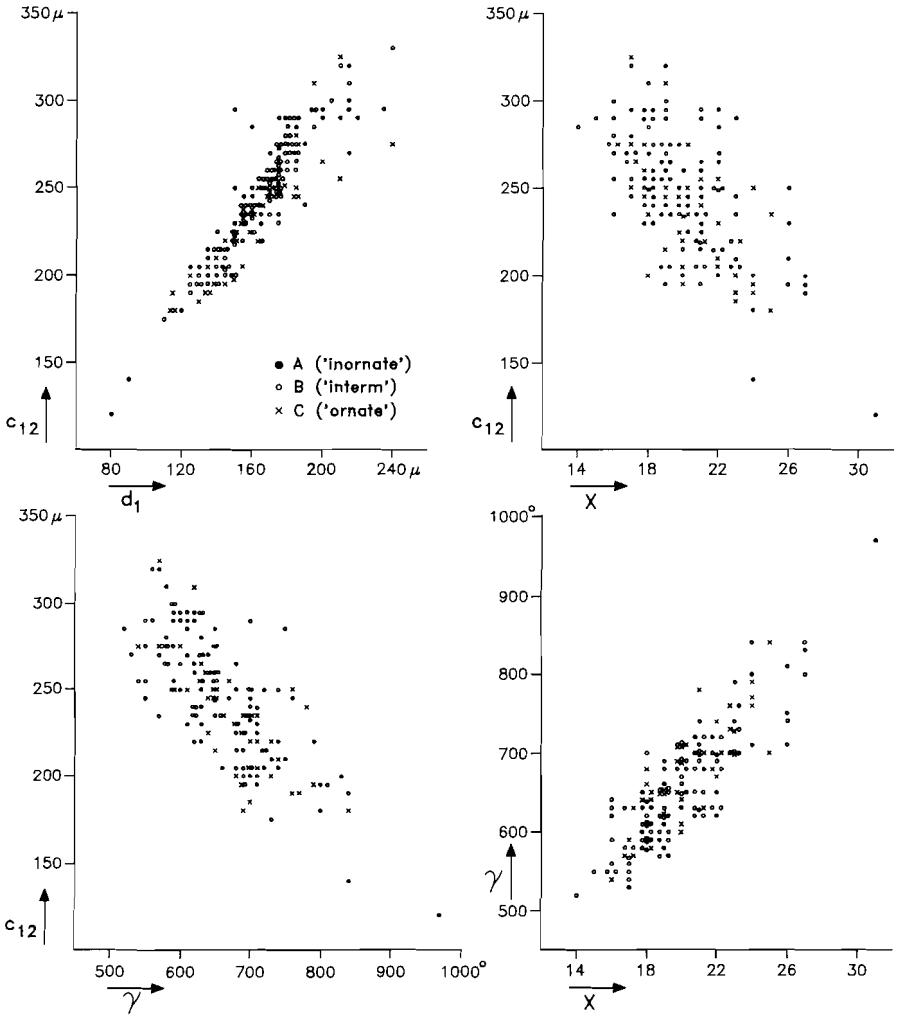

Figure 38: Scatter diagrams of data on selected parameter combinations in IR469 (*C. mediterraneus*) with indication of the morphogroups.

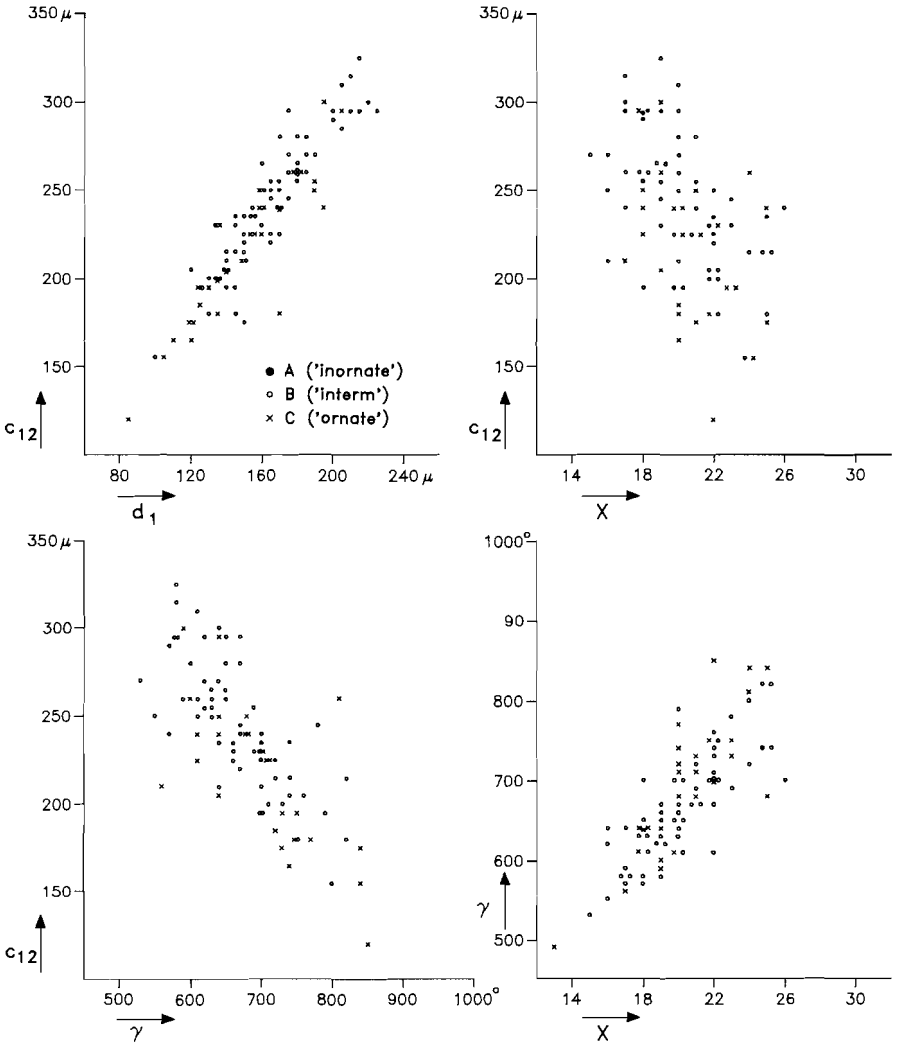

Figure 39: Scatter diagrams of data on selected parameter combinations in IR470 (*C. mediterraneus*) with indication of the morphogroups.

in most of the European samples no heterogeneity is apparent in the Ramla data.

Univariate analysis

The results of the univariate analysis are presented in Tables XV and XVI. The latter table contains values based on the standardized data sets and both

tables include the results of the calculations performed on all the Ramla observations together. Figure 40, containing partial mean parameter values (± 1 SE), shows the good correspondence between the data from both samples. In the intermediate groups embryon-size tends to be larger and the nepionic parameter values tend to be smaller than in the ornate and inornate groups. A fair number of these differences are significant or close to significance according to the results of Student's t-tests.

IR469 $\bar{d}_1$:	$t_{A-B} = -2.09$	df = 122	$p < 0.05$
$\bar{c}_{12}$:	$t_{A-B} = -2.30$	df = 120	$p < 0.05$
	$t_{B-C} = 2.67$	df = 127	$p < 0.01$
$\bar{X}$:	$t_{A-B} = 1.83$	df = 106	$p < 0.1$
$\bar{\gamma}$:	$t_{A-B} = 1.70$	df = 111	$p < 0.1$
	$t_{B-C} = -2.06$	df = 117	$p < 0.05$

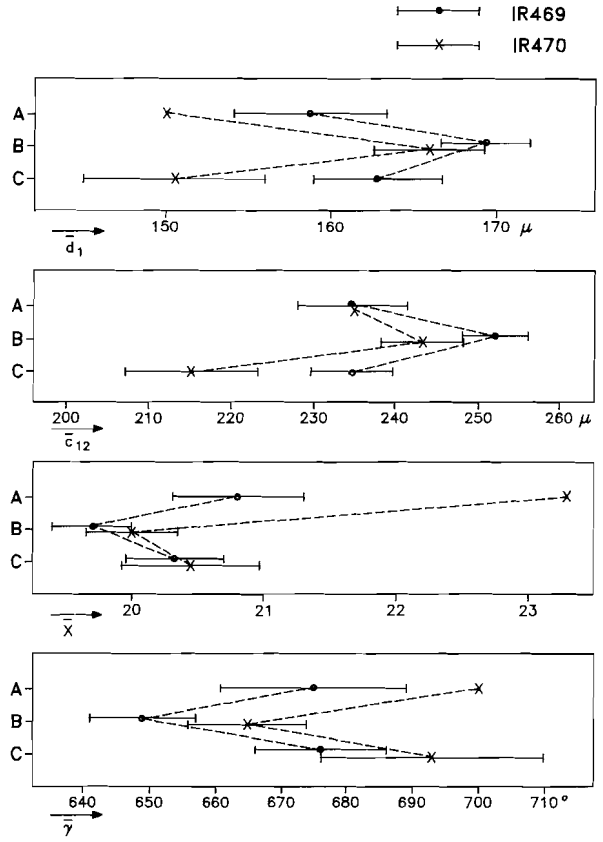

Figure 40: Mean parameter values (± 1 SE) of the morphogroups in IR469 and IR470 (*C. mediterraneus*).

IR470 $\bar{d}_1$:	t_{B-C} = 2.48	df = 89	$p < 0.02$
$\bar{c}_{12}$:	t_{B-C} = 3.12	df = 88	$p < 0.01$

As already noticed in our previous report and in contrast with the data on our European Cycloclypei, the differences in the embryon-size parameters appear to be more distinct than those in the nepionic parameters. If we lump the data of both samples, a similar pattern is found.

All data $\bar{d}_1$:	t_{A-B} = -2.14	df = 186	$p < 0.05$
	t_{B-C} = 2.64	df = 220	$p < 0.01$
$\bar{c}_{12}$:	t_{A-B} = -1.98	df = 184	$p < 0.05$
	t_{B-C} = 3.95	df = 217	$p < 0.001$
$\bar{X}$:	t_{A-B} = 2.26	df = 162	$p < 0.05$
$\bar{\gamma}$:	t_{B-C} = -2.54	df = 200	$p < 0.02$

These results are presented in figure 41 together with those for the total number of European data. In both data sets embryon-size tends to be larger in the intermediate groups with respect to the inornate groups, while the corresponding values of the nepionic parameters tend to be smaller. However, the differences in embryon-size are far more distinct in the Ramla data.

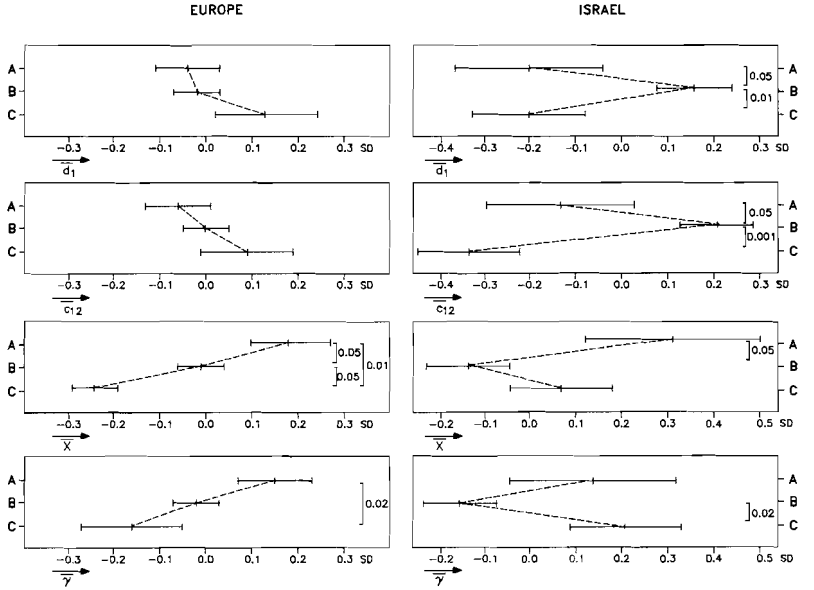

Figure 41: Standardized mean parameter values (± 1 SE) of the morphogroups based on the total number of data from Europe (left) and Israel (right). Significance levels of differences are indicated.

In the European specimens the differences in internal morphology for morphogroups B and C are similar to those observed for groups A and B. In the Ramla specimens the change from group B to group C is opposite to the one from group A to B. As a consequence the inornate and ornate morphogroups are quite similar with respect to their overall internal morphology and distinctly different from the intermediate group of specimens.

Bivariate analysis

For the parameter combinations d_1-X and d_1-γ the correlation coefficients within each sample were calculated for the single morphogroups and for the total number of observations. These results, together with those based on all the Ramla specimens together, are presented in Table XVII. It shows that no distinct differences are present in the correlation coefficients of either parameter pair; similar r values are found in the three morphogroups in both samples.

The European data revealed that, at any embryon-size level, more ornamented specimens tend to show fewer precyclic chambers and convolutions. In the scatter diagrams of c_{12}-X and c_{12}-γ in figure 42, containing all the Ramla observations, such a relation is not clearly present, which may be due to the large numbers of data.

The clusters in the scatter diagrams of both parameter pairs were split into

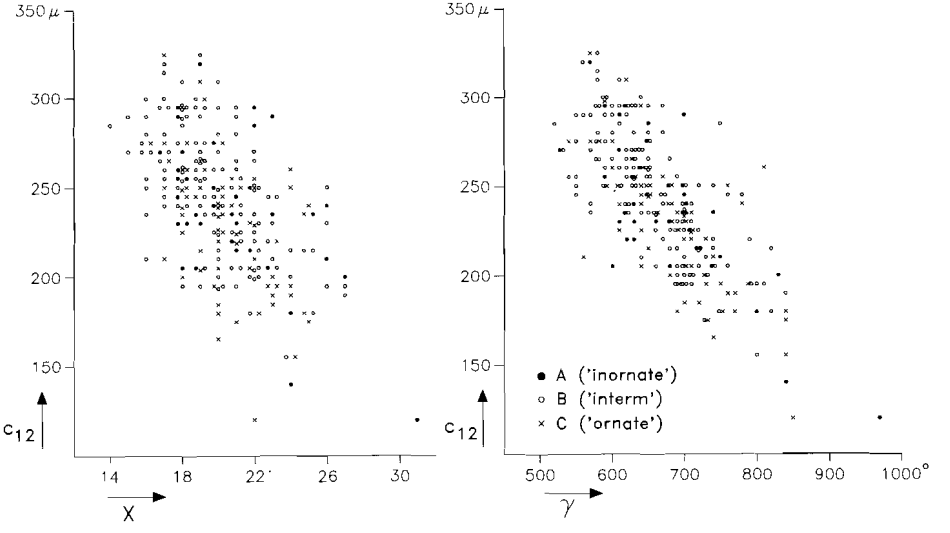

Figure 42: Scatter diagrams of all Ramla data (*C. mediterraneus*) on the parameter pairs c_{12}-X and c_{12}-γ.

smaller portions, in the way described in the earlier section on the European Cycloclypei; the observations on the inornate and intermediate specimens were lumped. In figure 43 bivariate means are plotted which respectively represent the ornate specimens and the specimens of our lump category within these portions. The relative position of the points provides little or no evidence for differences in the relation between embryon-size and nepionic configuration linked to external morphology. In the $\bar{c}_{12}$-$\bar{X}$ diagram the lower two points representing the ornate specimens are observed to plot to the left (i.e. in the direction of smaller X values) of the corresponding points of the other morphotypes. Although these differences in $\bar{X}$ are of the same type and magnitude as those found in the European data set, they are not as reliable due to the relatively small number of observations. We would need more data still, especially on the ornate morphotypes, to arrive at more firmly based conclusions.

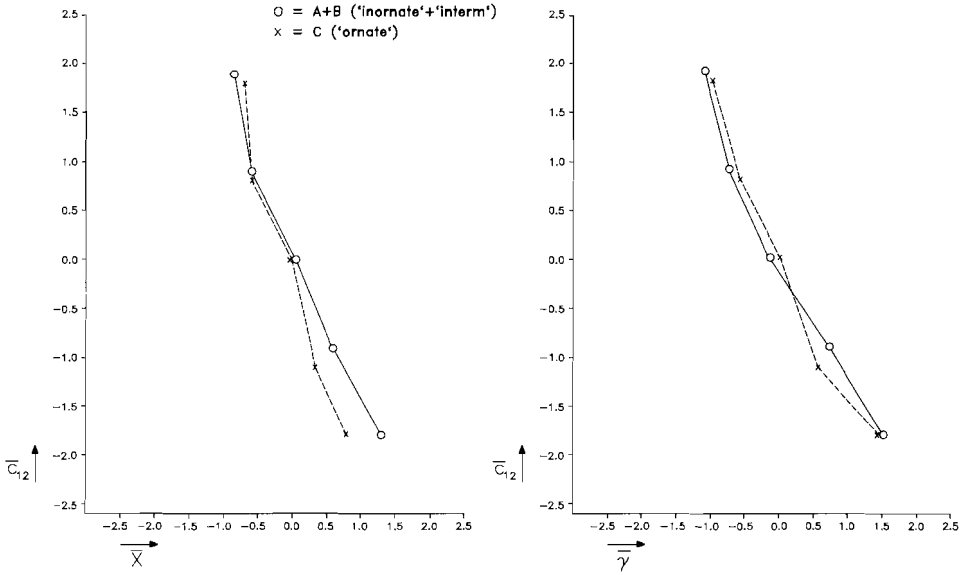

Figure 43: Plots of the bivariate mean values of the parameter combinations c_{12}-X and c_{12}-γ for successive c_{12} intervals of the standardized Ramla data set (*C. mediterraneus*). Boundaries coincide with the values of -2.5, -1.5, -0.5, +0.5, +1.5 and +2.5 on the c_{12} scale.

V.4 THE SIZE OF THE NEPIONIC STAGE

As reported in the previous chapter the maximum diameter of the nepionic stage, D_X, has been determined in a restricted number of samples only. In the

set of samples in which the external morphology was studied as well, D_X values are available on SP707, SP729 (one split), SP818, SP825, SP842, JT7911, IR469 and IR470. The data on SP818, SP825 and SP842 were lumped. With respect to the other parameters the total number of observations on D_X is small. Particularly in the more primitive of these assemblages (e.g. SP729) D_X could be measured in a small part of the specimens only. Therefore the number of observations in the separate morphogroups is reduced as well, which seriously hampers the statistical analysis of the data.

Table XVIII contains the mean D_X values for each morphogroup in the Spanish and Italian samples. The calculations for the Lanuza lump sample were performed on the standardized data set only; for the other three samples the results are presented in real values as well.

Although exceptions are clearly present, the mean diameter of the nepionic stage tends to decrease from the inornate to the ornate morphogroups. A significant difference is even recorded for the inornate and intermediate groups in the assemblage of SP707 (t_{A-B}: 3.11, df: 140, $p < 0.01$).

The partial mean values of D_X in these European samples are entered in the scatterdiagram of figure 44 together with those of parameter c_{12}. The inornate

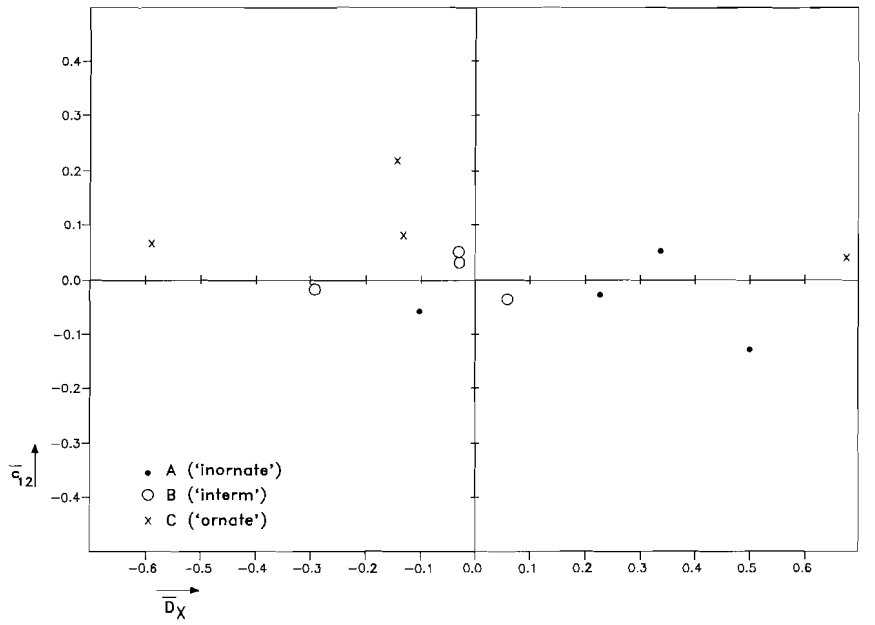

Figure 44: Scatter diagram of standardized mean values of parameters c_{12} and D_X of the three morphogroups in the European samples.

morphogroups (A) plot toward the side of the diagram for large mean values of D_X. The data on group B occupy an intermediate position and the ornate morphogroups tend to plot in the part of the diagram for small mean values of D_X. One exceptional, large value is recorded for the ornate morphogroup in SP729 but it is based on only three observations.

We lumped all standardized data on our European Cycloclypei and recalculated the partial mean D_X values of the three morphogroups. The results are included in Table XVIII. The mean size of the nepionic stage is significantly larger in the inornate morphogroup than in the intermediate group or in the ornate group of specimens (t_{A-B}: 2.66, df: 240, $p < 0.01$; t_{A-C}: 2.18, df:163, $p < 0.05$). The difference between the intermediate and ornate morphogroup is not significant in this lumped data set. However, our diagram in figure 44 did leave the impression that also the partial mean D_X values of the intermediate groups tend to be larger than those of the ornate groups.

This suggests that in the European Cycloclypei the size of the nepionic stage tends to be smaller as the ornamentation of the test is more developed.

Table XIX contains the partial mean D_X values of the morphogroups in the Ramla samples. The differences in the mean nepionic diameters of the groups appear to be rather small and statistically not significant. Moreover, the changes in D_X from one morphogroup to the other do not follow the same pattern in the two samples from this locality. The recorded differences are therefore ascribed to chance. So, in contrast to the case of the European Cycloclypei no real differences in nepionic size can be detected in the data on the Ramla morphogroups.

In an earlier part of this chapter we concluded that in our European assemblages ornamented specimens tend to show fewer precyclic chambers than specimens with corresponding embryon dimensions, but with a less distinctly developed ornamentation. For the Ramla specimens such a difference could not be substantiated. These conclusions show some resemblance to the present ones on parameter D_X. Also in this parameter differences related to ornamentation could be recorded in the European Cycloclypei only. This may be understood if we accept that parameter X is an estimate for the number of growth steps, necessary to arrive at the test size, estimated by parameter D_X. A smaller size of the precyclic stage simply tends to reduce the number of these growth steps if embryon-size is kept constant.

For the parameter combinations d_1-D_X and X-D_X we calculated the partial correlation coefficients within the morphogroups of each assemblage. However, these calculations were in large part performed on small numbers of observations only. This may well be the reason that the resulting r values are

rather variable. In the case of the X-D_X combination a significant correlation is recorded in a restricted number of cases only. As no decisive conclusions could be drawn from these data and no consistent differences were suspected to be present in the r values of the morphogroups in the first place, we decided not to include this part of the statistical analysis in our presentation.

V.5 CONCLUSIONS

Cosijn's distinction of an inornate and an ornate *Cycloclypeus* lineage in the Spanish Oligocene is considered to be based on invalid data. No more than one *Cycloclypeus* species can be recognized in any of our Mediterranean Oligocene samples.

Cycloclypei of the *droogeri* lineage have a smooth to ornamented external appearance. Following the hypothesis of Drooger and Roelofsen (1982) these differences in external morphology are considered to be ecophenotypic and related to differences in depth of habitat.

As further suggested by Drooger and Roelofsen (op.cit.) a relation is present between external and internal morphology in the European assemblages of the *droogeri* lineage. Ornate morphotypes tend to have fewer precyclic chambers than less ornamented specimens. Furthermore, the number of convolutions is generally smaller in ornate than in inornate ones. The size of the embryon tends to be larger in more ornamented specimens but the recorded differences are not significant in the statistical sense.

At any embryon-size level the numbers of precyclic chambers are generally smaller in more ornamented specimens. Such differences are equally apparent though less distinct in the numbers of convolutions. Therefore diferences in nepionic characters, which are related to differences in external morphology, do not merely result from differences in embryon-size, as was suggested by Drooger and Roelofsen (op. cit.).

From our data from Israel it is concluded that in the Ramla Cycloclypei differences related to external morphology are more distinct in embryon-size than in nepionic characters. Moreover, embryon-size is found to be larger in specimens with an intermediate external morphology with respect to other, more ornate or inornate specimens. Such moderately ornamented specimens tend to show fewer precyclic chambers and fewer convolutions although not all of these differences are of the same statistical significance.

Data suggest that in the European Cycloclypei the size of the nepionic stage tends to be smaller in more ornamented morphotypes. In the Cycloclypei from Ramla such diferences were not recorded. We suggest that in our European assemblages the overall smaller numbers of precyclic chambers and convolutions in more ornamented specimens are partly due to the overall smaller size of the nepionic stage in these specimens.

Chapter VI

ONTOGENETIC DEVELOPMENT

VI.1 INTRODUCTION

Data on parameters O_i, A_j, E_i and k_j, which relate to the early ontogenetic development of *Cycloclypeus* individuals, are available on Ramla specimens only. The first three of these parameters were determined for each budding-step starting from the 3-chambered embryonic stage onward ($i = 3$) up to and including the stage of the first cyclic chamber ($i \leq X + 1$). Since parameter k_i denotes the surface area of the test in median section relative to the area of the preceding stage, values on this parameter are available from the 4-chamber stage onward only ($4 \leq i \leq X + 1$).

This set of parameters could be determined in only 70 of the total number of 264 specimens from both the Ramla samples. In the other specimens the suite of chambers to be measured is only partly preserved. For this small sample we calculated mean values of parameters d_1, c_{12}, X, γ and D_X which were not significantly different from those based on the data set of all Ramla specimens together. Therefore our selection of specimens is thought to represent the Cycloclypei of this locality sufficiently well.

VI.2 THE DATA

Histograms, which are not reproduced here, were drawn for parameters O_i, A_j, E_i in the interval of $3 \leq i \leq 17$ and for parameter k_i in the interval of $4 \leq i \leq 17$. In only one of these 59 distributions a distinct bimodality was observed. The relevant parameter, E_{13}, measures the degree in which the 13th chamber embraces the preceding part of the test. However, the bimodality in this distribution is ascribed to chance. In Table XX mean values are entered for the parameters O_i, A_j, E_i and k_j. No data are presented on the stages from the 18th chamber onward as increasing numbers of specimens become removed from our statistical sample as in these specimens the stage of the second cyclical chamber is reached. Two specimens reach this stage already after 16 and 17 chambers, respectively.

The mean values of parameter O_i and parameter A_j, which measure the perimeter and the surface area of the test after each buddingstep, respectively, show an exponential increase in the course of the ontogenic interval investigated. The mean perimeter values, $\bar{O}_i$, are entered in figure 45. The mean

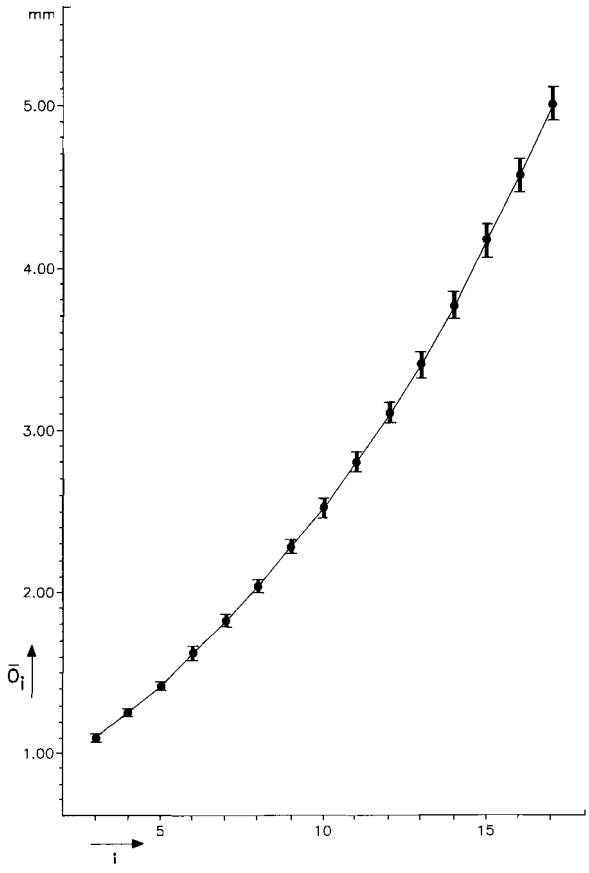

Figure 45: Mean values (± 1 SE) of parameter O_i in the early ontogenetic stages (i = 3 - 17) of *C. mediterraneus* from Ramla.

values for the degree of embracement, $\bar{E}_i$, are entered in figure 46. It shows the low value for chamber number 3, which is considered to be part of the embryonic stage. The first nepionic chamber shows a strong increase in relative length but, culminating at the stage of i = 7, a dent is observed in the line connecting the successive mean values. From this stage onward the mean values for the degree of embracing show a regular increase.

Parameter k_i shows a decrease in mean values for the larger part of the ontogenetic interval we studied. This means that the relative increase in size of the test at each budding-step showed a tendency to become smaller as a *Cycloclypeus* individual grew older. From figure 47, which contains the mean

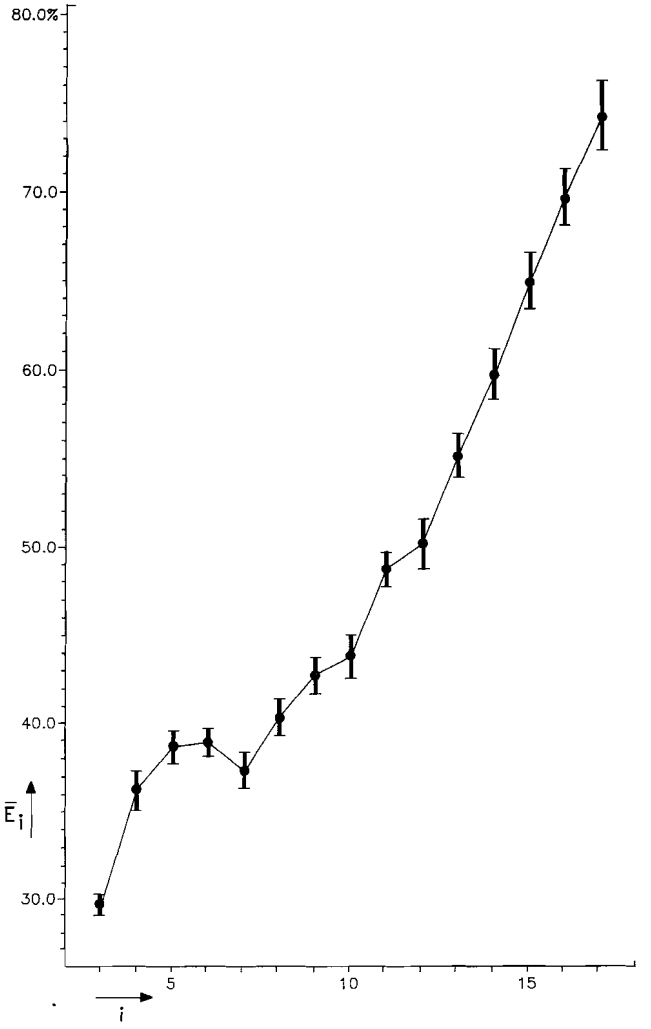

Figure 46: Mean values (± 1 SE) of parameter E_i in the early ontogenetic stages (i = 3 - 17) of *C. mediterraneus* from Ramla.

values of k_i, it appears that this decrease is not a regular one. A conspicuous, large drop in the mean values is apparent from the stage of i = 6 to the stage of i = 7. Furthermore, the aforementioned reduction in mean k_i values does not seem to be valid for the first three nepionic chambers, up to the stage of i = 6, as in this interval invariably large values are recorded.

Two different phases seem to be present in the ontogenetic interval studied.

The early one is characterized by relatively large growth steps and a waning degree of embracement. In the later phase growth steps are markedly smaller and tend to decrease even further with increasing age, while the degree of embracement shows a fairly regular increase. On average this second phase begins with chamber number 7 at which stage also a relatively small mean value for parameter E_i was recorded. These conclusions, based on average sample values, are in large part confirmed by inspection of the individual specimens. It appears that one of the chambers near the stage of i = 7 may indeed be relatively short with regard to the adjoining ones, although in other specimens such a difference is less distinct if present at all.

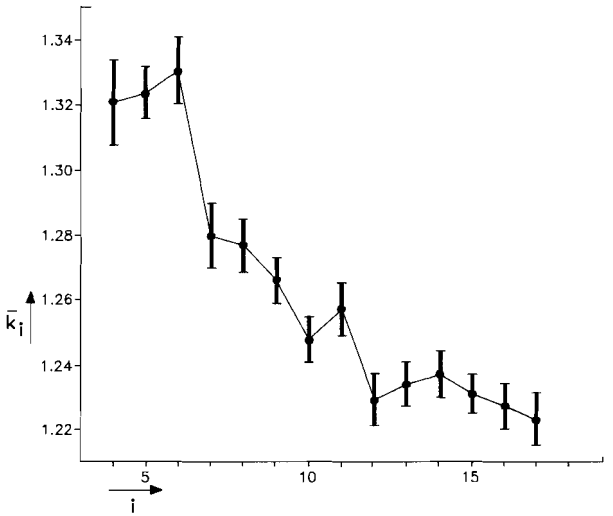

Figure 47: Mean values (± 1 SE) of parameter k_i in the early ontogenetic stages (i = 4 - 17) of *C. mediterraneus* from Ramla.

Correlation coefficients were calculated for parameter O_i combined with parameters c_{12}, X, γ, D_X, E_i, k_i; for parameter E_i combined with parameters c_{12}, X, γ, D_X, k_i and for parameter k_i combined with parameters c_{12}, X, γ, D_X. Correlation coefficients are also available on the combinations of parameters O_i, E_i and k_i with $\bar{k}$, representing the mean of all k_i values in individual specimens in the interval of $4 \leq i \leq 17$. This statistic $\bar{k}$ is an estimate for the mean rate of test-size increase of each specimen in the interval studied. For all combinations involving parameter k_i, r values are calculated for all stages in the interval of $4 \leq i \leq 17$; for all other combinations this interval includes the stage of i = 3 ($3 \leq i \leq 17$). The r values are listed in Table XXI;

with exception of the values of the combinations involving parameter γ, they are presented graphically in figures 48, 49 and 50.

O_i-c_{12}: At the stage of i = 3 both parameters in this combination are estimates for the size of the (3-chambered) embryon, c_{12} being a measure for one of its diameters and O_3 for its perimeter. The recorded r value at this stage is therefore very high (figure 48); in later stages r values are still quite high but show a steady decrease. This indicates that specimens with large embryons tend to remain large in later stages as well. In these later stages, however, other factors than embryon-size, like rate of growth, seem to become of increasing importance for the size of the individuals.

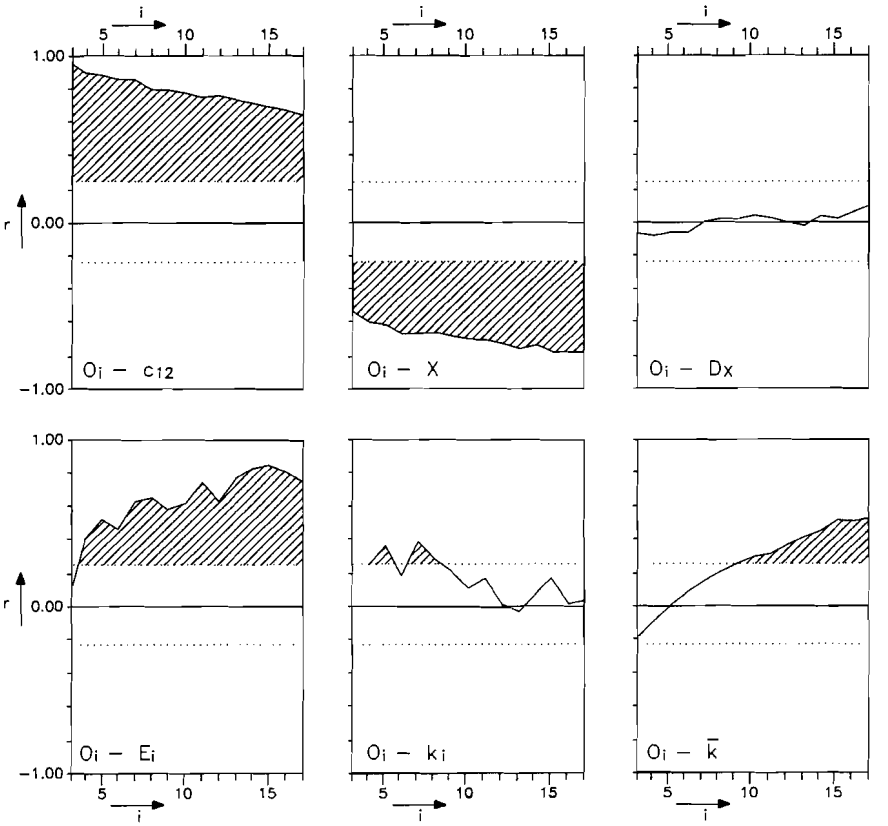

Figure 48: Plots of r values for parameter combinations involving O_i in *C. mediterraneus* from Ramla. Shaded areas: significant values at the level of p = 0.05.

O_i-X: For this combination a distinct negative correlation is observed, which steadily becomes stronger in the later stages. Larger specimens tend to reach the stage of cyclic growth in a smaller number of steps.

O_i-D_X: No significant correlations are recorded for this combination: A large stage i is not associated with a large precyclic stage, as the stage of cyclical growth is reached in a smaller number of growth steps (O_i-X).

O_i-E_i: For i = 3 this combination shows us the relation between the perimeter of the (3-chambered) embryon and the degree in which the third chamber embraces the two earlier ones. In contrast to the r values in later stages, this one is exceptionally small and even not significant. This further supports our earlier conclusion that the third chamber is part of the embryonic stage in *Cycloclypeus* and quite different from the later, nepionic chambers.

In the later stages the r values tend to reach increasingly higher, positive values. As the degree of embracing is calculated from the perimeter of the test by $E_i = L_i/O_i$, one might have expected any correlations to be negative. But in large specimens a larger part of the perimeter is covered by the last chamber in each stage, in spite of the fact that this perimeter is larger. Apparently, the degree of embracing is related to the size of the test and more strictly so in the later stages of the ontogenetic interval studied.

O_i-k_i: Most of the r values recorded for this parameter combination are positive. However, a significant level is reached by only a few of them in the early part of the interval studied. Apparently, one large growth step may have had but little effect on the size of that particular stage as it may have been preceded by a number of smaller ones. In the early stages, however, a single large step may have been of more significance.

O_i-$\bar{k}$: A steady increase in r values is recorded for this combination, resulting in significant, positive correlations in the later part of the interval studied. In early stages size is primarily related to the dimensions of the embryon. However, in the course of ontogeny the average rate of size increase, $\bar{k}$, is of increasing importance for the size of the test.

The size of the test at stage i is dependent on initial size (O_i-c_{12}) and on rate of size increase (O_i-$\bar{k}$). At a large test-size there is a high degree of embracement (O_i-E_i). Therefore large specimens reached the stage of cyclic growth (E_i = 100%) in a small number of growth steps (O_i-X).

Correlation coefficients of combinations involving parameter E_i are presented in figure 49.

E_i-c_{12}: For the stage of i = 3 again an exceptionally small r value is recorded; the size of the embryon has no relation with the degree of embracing of its last chamber. In the later, nepionic stages size and degree of embracing are positively correlated. This relation is probably connected with two earlier ones. Specimens with

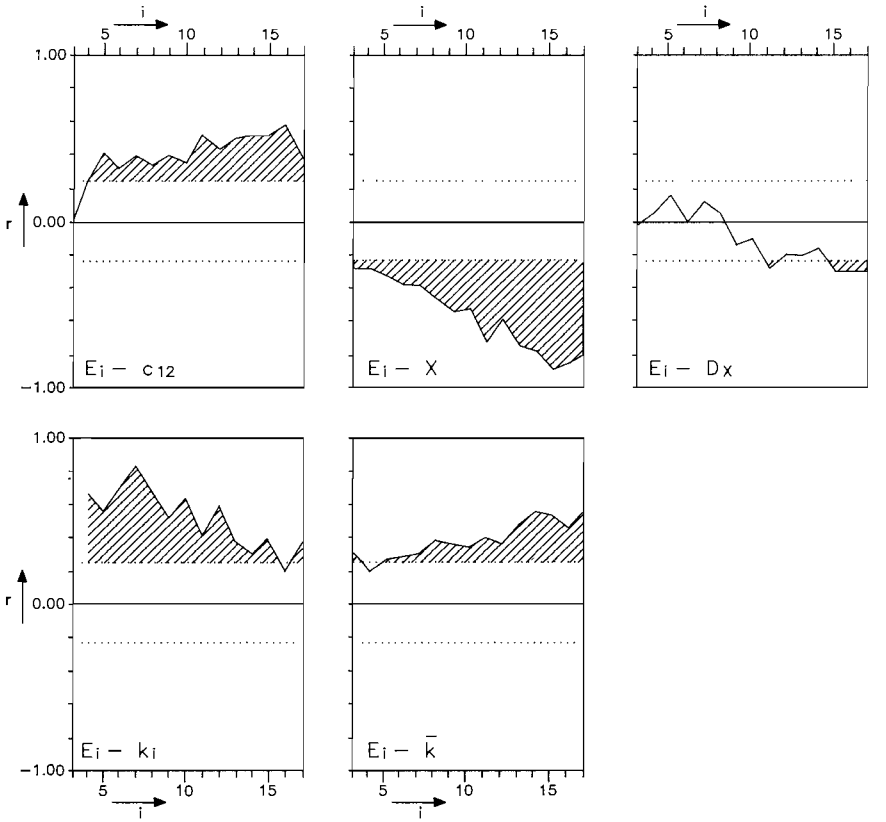

Figure 49: Plots of r values for parameter combinations involving E_i in *C. mediterraneus* from Ramla. Shaded areas: significant values at the level of p = 0.05.

relatively large embryons tend to be larger in later stages as well (O_i-c_{12}) and therefore tend to reach higher degrees of embracing in the succession of chambers (O_i-E_i).

E_i-X: The r values for this combination are negative; the correlation rapidly becomes stronger in the later ontogenetic stages. In specimens, showing a high degree of embracement in the successive stages, the stage of total embracement (cyclical growth) tends to be reached in a small number of steps. This relation is stronger (more direct) as the number of steps between i and X becomes smaller.

E_i-D_X: Weak, negative correlations are recorded for this combination in the later stages only. In these stages a relatively high degree of embracing tends to occur in specimens which are small upon reaching the stage of cyclical growth.

E_i-k_i: In the early stages a strong, positive correlation is recorded for this combination. In the later stages r values drop to lower, but in most cases still significant levels. So, although a single large growth step did not always lead to a relatively large size (O_i-k_i), it generally did lead to a relatively high degree of embracing, i.e. to the formation of a relatively long chamber during that step.

The recorded reduction in r values in the course of ontogeny is complementary to the earlier discussed increase in the r values of the O_i-E_i combination. This seems to indicate that in the early stages the degree of embracing is more directly related to the size of the individual growth steps whereas in the later stages the size of the test seems to be of increasing importance in this respect.

E_i-$\bar{k}$: The r values for this combination are positive, reaching significant levels for nearly all stages investigated. As in the O_i-$\bar{k}$ combination, an overall increase in r values is recorded in the course of ontogeny. A large average rate of size increase may have led to a large size (O_i-$\bar{k}$) and, accordingly, to a high degree of embracement (O_i-E_i). However, the relation between average rate of size increase and size of the test became apparent only in the later part of the ontogenetic development. Therefore a second factor seems to be of importance for the degree of embracing, which probably is the size increase at single growth steps, k_i. These steps tend to be larger in specimens with high average rates of size increase (k_i-$\bar{k}$) and larger steps tend to result in relatively

longer chambers, i.e. chambers showing a higher degree of embracing (E_i-k_i).

Specimens showing large embryons or high rates of size increase tend to be larger (O_i-c_{12},O_i-k_i, O_i-$\bar{k}$) and as large specimens tend to have more embracing chambers (O_i-E_i), embryon-size and rates of size increase are related to the degree of embracing as well (E_i-c_{12},E_i-k_i, E_i-$\bar{k}$)

In figure 50 r values are presented of combinations involving parameter k_i.

k_i-c_{12}: This parameter pair combines our estimates for embryon-size and the relative size of individual growth steps. All of the r values recorded are ascribed to chance, although a significant level is

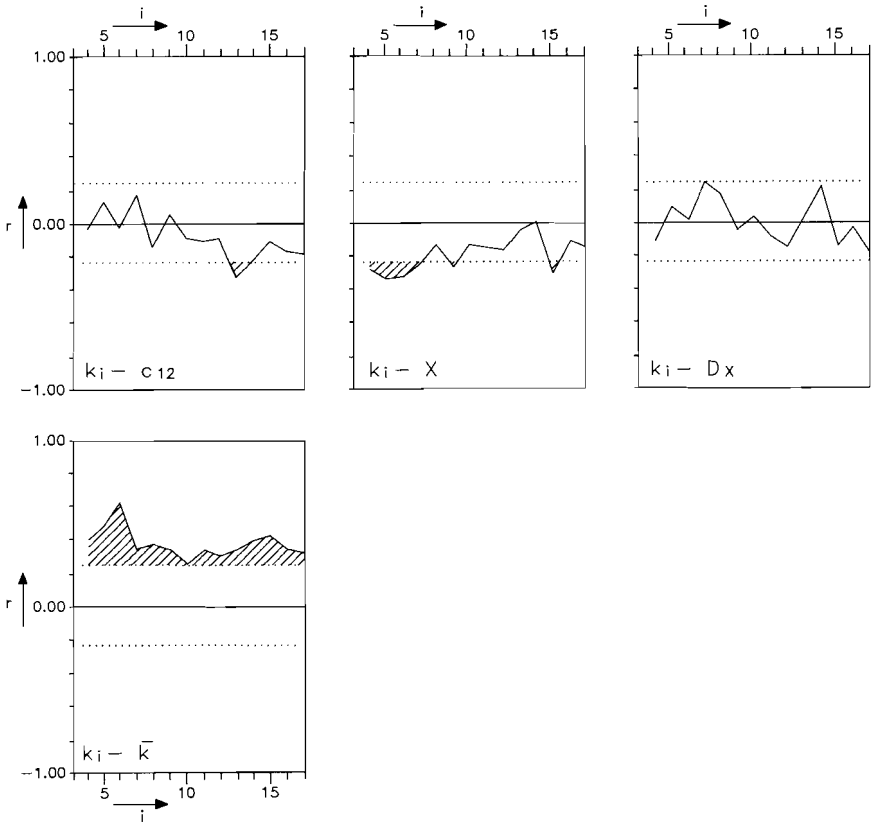

Figure 50: Plots of r values for parameter combinations involving k_i in *C. mediterraneus* from Ramla. Shaded areas: significant values at the level of p = 0.05.

reached by one of them. Moreover, no significant correlation is recorded for the combination of $\bar{k}$-c_{12} ($r = -0.15$, $n = 70$): No relation appears to be present between embryon-size and mean rate of relative size increase either.

k_i-X: Nearly all of the r values for this combination are negative but significant levels are only reached in the early nepionic part, up to the stage of $i = 6$, and in the later stage of $i = 15$. So, the number of steps in the precyclic stage tends to be reduced by a large growth step, particularly when it occurs in an early nepionic stage. An equally negative but more distinct correlation is recorded for the $\bar{k}$-X combination ($r = -0.51$, $n = 70$, $p < 0.01$): Specimens with a high mean rate of size increase tend to reach the stage of cyclic growth in a small number of steps.

High rates of size increase and, consequently, large test size (O_i-k_i, O_i-$\bar{k}$) result in more embracing chambers (O_i-E_i) and an earlier achievement of total embracement (E_i-X).

k_i-D_X: For this combination of parameters no significant correlations are recorded: One large growth step did not lead to a larger ultimate size of the precyclic stage. Moreover, no significant correlation is recorded for the $\bar{k}$-D_X combination ($r = 0.01$, $n = 70$), which means that specimens with a high mean rate of size increase did not build a larger precyclic stage either. Large growth steps simply reduced the number of steps necessary to achieve cyclic growth (k_i-X, $\bar{k}$-X).

k_i-$\bar{k}$: In single specimens the size increase at each stage i (k_i) is positively correlated with the specimens' mean rate of size increase as calculated from all its k_i values in the interval of $4 \leq i \leq 17$. These correlations are significant but the r values are rather small: In specimens showing a relatively high mean rate of size increase, as expressed by large $\bar{k}$ values, not all of the growth steps k_i are equally large. In fact, k_i values are, as a rule, significantly correlated in successive buddingsteps only.

In chapter IV we discussed the positive correlation between parameters X and D_X. If this correlation indicates that the size of the precyclic stage depended upon the number of nepionic growth steps, it might be assumed that the size of the precyclic stage then also depended upon the size of these steps. An important result of the present analysis therefore seems to be that such a relation between the size of growth steps (k_i and $\bar{k}$) and the size of the precyclic stage (D_X) is absent.

As already suggested in the earlier discussion the positive correlation between X and D_X more probably reflects a reversed relation, in which the number of growth steps depended on the ultimate size of the precyclic stage. This is furthermore supported by the negative correlation between $\bar{k}$ (k_i) and X. Larger growth steps tend to reduce the number of steps necessary to reach this ultimate size, estimated by our parameter D_X.

If the achievement of cyclical growth thus was dependent upon a critical size of the test, it would be no more than a specific case of a more general relation existing between the size of the test at some stage i and the degree of embracing of the ultimate chamber in that stage (O_i-E_i). Particularly in the later part of the nepionic phase this degree of embracing becomes strongly related to the size of the test.

VI.3 ORNAMENTATION AND ONTOGENETIC DEVELOPMENT

Table XXII contains the partial mean values of parameters O_i, E_i, A_i and k_i for the three morphogroups in the Ramla assemblages. In figure 51 we entered the mean values of parameter O_i, measuring the perimeter of the test after each buddingstep. It shows that from the embryonic stage i = 3 onward the specimens of the intermediate group tend to be larger than inornate and ornate specimens. In the entire interval from i = 3 to i = 17 the differences in mean values of O_i for the intermediate and ornate morphogroups are significant or on the verge of significance ($1.95 \leq t_{BC} \leq 2.55$; $53 \leq df \leq 55$; $p < 0.1$ to $p < 0.02$). The differences in the mean values of the intermediate and the inornate group are not significant. The data on parameter A_i, measuring the area of the test instead of its perimeter, are quite similar to those on parameter O_i and are therefore not presented separately.

The partial mean values for the degree of embracement, E_i, are entered in figure 52. For all three groups the increase in the mean values is interrupted at the stage of i = 7, which is already more or less apparent at the preceding stage of i = 6. This interruption was already observed in the mean values of all specimens together. From this stage of i = 7 onward the chambers in the group of the intermediate specimens tend to be more embracing than the corresponding chambers in the other groups but no significant differences are recorded.

From the stage of i = 6 to the stage of i = 7 a conspicuous, large drop was apparent in the mean values of all k_i observations together (fig. 47). Figure 53 shows that such a drop occurs in the mean values of the separate groups as well. Furthermore, in the further ontogenetic reduction of the k_i values similar though rather irregular patterns are followed by the three morphogroups.

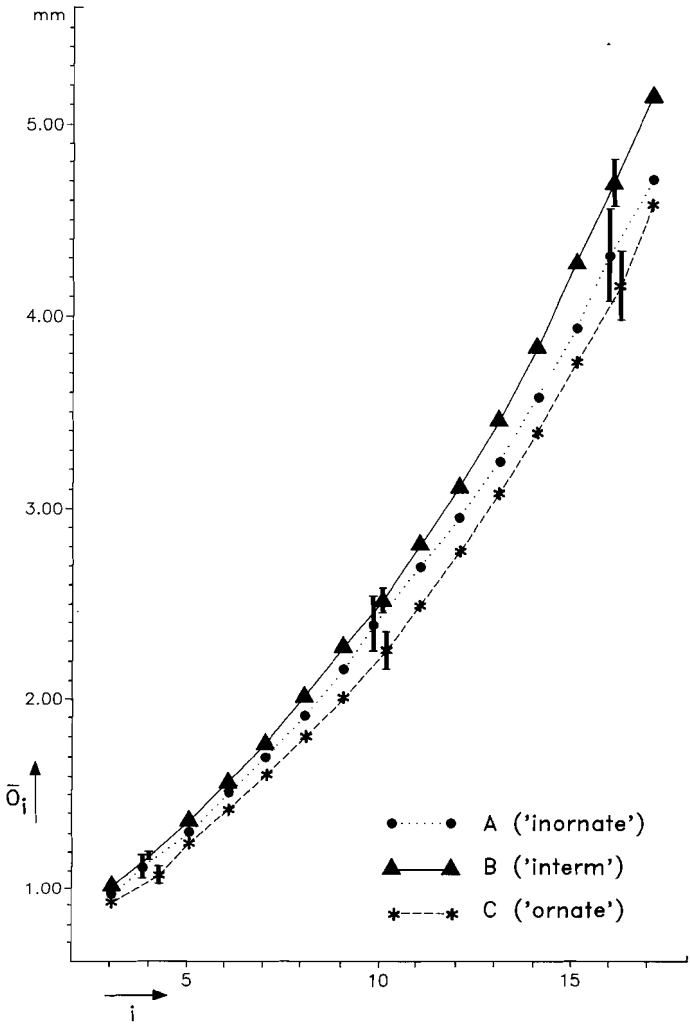

Figure 51: Plot of the partial mean values of parameter O_i ($3 \leq i \leq 17$) of the morphogroups in *C. mediterraneus* from Ramla. Intervals of $O_i \pm 1$ SE are indicated for the stages of i = 4, i = 10 and i = 16.

However, small differences between the groups seem to be present:

- The intermediate group tends to show relatively large $\bar{k}_i$ values for the entire interval studied but the differences with the other groups are small and significant in one case only in $\bar{k}_9$ for the intermediate and the ornate group of specimens ($t_{B\text{-}C}$: 2.60, df: 55, $p < 0.02$).
- In the early part of the nepionic stage the ornate group shows small $\bar{k}_i$

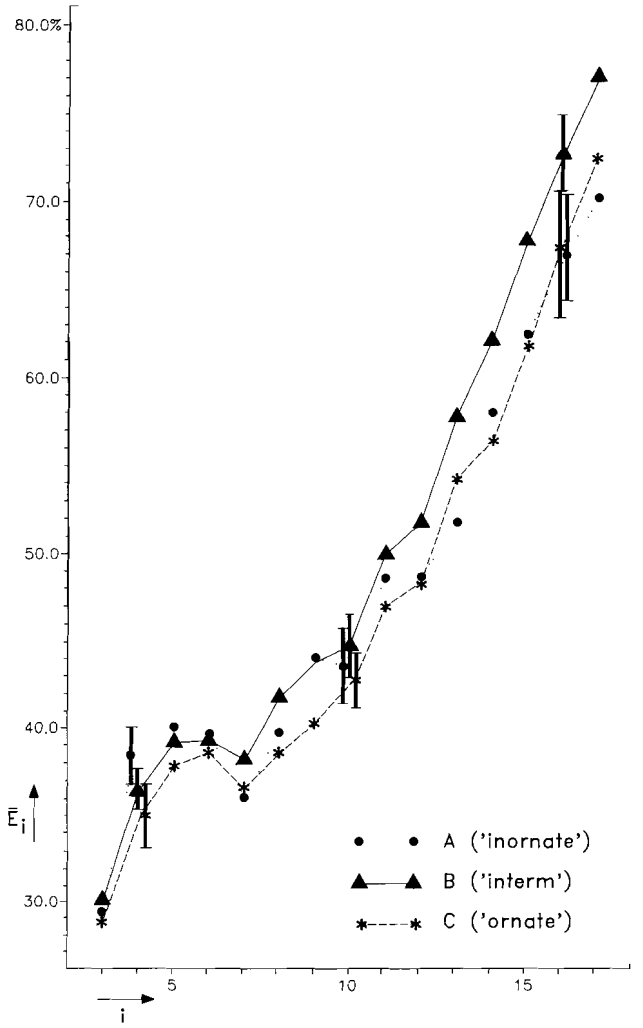

Figure 52: Plot of the partial mean values of parameter $\bar{E}_i$ ($3 \leq i \leq 17$) of the morphogroups in *C. mediterraneus* from Ramla. Intervals of $\bar{E}_i \pm 1$ SE are indicated for the stages of i = 4, i = 10 and i = 16.

values with regard to the other groups but these differences are not significant.

- In the later part of the nepionic stage ($i > 12$) relatively small $\bar{k}_i$ values are shown by the inornate group. The difference in the values of $\bar{k}_{17}$ are nearly significant at the level of $p = 0.05$ for the inornate and the ornate morphogroups ($t_{A\text{-}C}$: -1.98, df: 32).

We further evaluated the differences in parameter k for the morphogroups by calculating the partial means for all k values in the ontogenetic interval studied. However, as the k values of the early stages are not comparable to those of the later stages, at each stage i k_i values were standardized for the complete data set ($\bar{k}_i$ = 0.000, SD_i = 1.000). The results listed below refer to all data in the interval $4 \leq i \leq 17$.

	N	$\bar{k}$	SD	SE
Group A (inornate):	182	-0.092	1.029	0.076
Group B (interm.) :	501	0.081	0.958	0.043
Group C (ornate) :	294	-0.081	1.022	0.060

These data confirm that in the interval concerned the intermediate specimens tend to increase in size with larger steps than the inornate and ornate specimens. If these differences are tested by means of a t-test, they appear to be significant at the level of p = 0.05 (t_{A-B}: -2.06, df: 681; t_{B-C}: 2.25, df: 793).

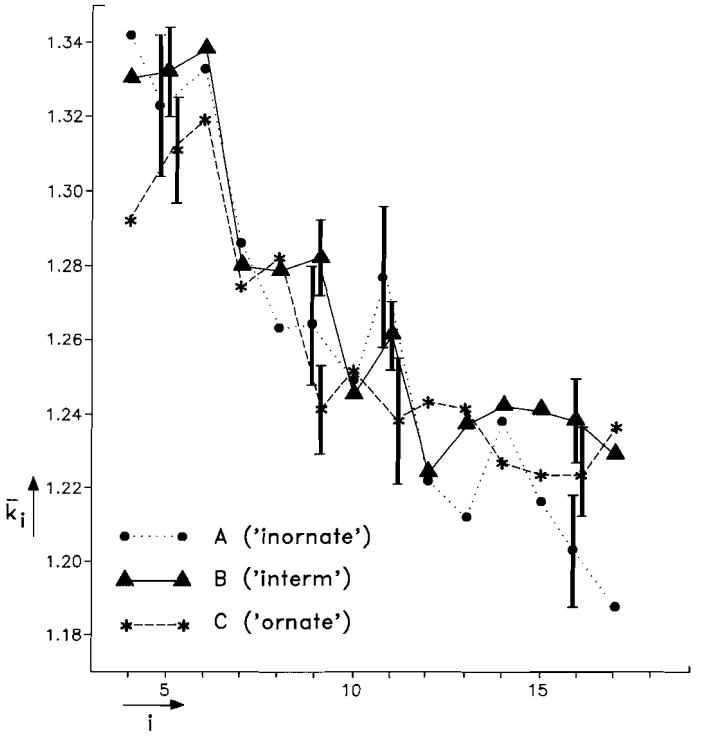

Figure 53: Plot of the partial mean values of parameter k_i ($4 \leq i \leq 17$) of the morphogroups in *C. mediterraneus* from Ramla. Intervals of $k_i \pm 1$ SE are indicated for the stages of i = 5, i = 9, i = 11 and i = 16.

One might raise the objection that, in theory, such statistical tests are not suited to evaluate these differences. All elements in a proper statistical sample should be randomly selected from the statistical population considered. In the present case, however, each k value is associated with 11 to 13 other k values; together these elements represent a suite of growth steps in a single *Cycloclypeus* specimen. Fortunately, however, these k values are not very well correlated. As mentioned in the previous section, r values are low and tend to be significant only for k values of successive budding-steps (k_i-k_{i+1}). Usually, no relation is apparent anymore between the size increase at one stage and the increase at the stage reached after two more buddingsteps (k_i-k_{i+2}). We therefore think that our testing procedure suites our purpose sufficiently well and that reliable results are produced.

As two different growth phases were distinguished in the ontogenetic interval studied, similar tests were conducted for the standardized k_i values of the three morphogroups in the intervals of $4 \leq i \leq 6$ and $7 \leq i \leq 17$ separately.

$4 \leq i \leq 6$	N	$\bar{k}$	SD	SE
Group A (inornate):	39	0.065	0.966	0.155
Group B (interm.) :	108	0.094	1.018	0.098
Group C (ornate) :	63	-0.201	0.958	0.121
$7 \leq i \leq 17$	N	$\bar{k}$	SD	SE
Group A (inornate):	143	-0.135	1.044	0.087
Group B (interm.) :	393	0.078	0.941	0.047
Group C (ornate) :	231	-0.048	1.039	0.068

The early three nepionic growth steps tend to be smaller in the ornate specimens than in the specimens of the other groups. The difference for group B and group C is close to the significance level of $p = 0.05$ ($t_{B\text{-}C}$: 1.87, df: 169). If the inornate and intermediate specimens are lumped, the difference for this lumped group and group C is even on the verge of significance ($t_{AB\text{-}C}$: 1.93, df: 208).

In the later stages of the nepionic development the growth steps tend to be smaller in both the ornate and inornate group of specimens with regard to the intermediate group but a significant level is reached only in the comparison with the inornate group ($t_{A\text{-}B}$: -2.25, df: 534, $p < 0.05$).

From figure 51, showing the mean values of parameter O_i, it was already apparent that at each stage i the specimens of the intermediate group tend to be larger than those of the other groups. It has now become clear that this is not merely the result of the larger dimensions of the initial stages of this group but

also of its tendency to add larger chambers. The curves representing the inornate and ornate groups start at a lower level due to the smaller mean embryon dimensions in these groups. Yet, in the early stages the curve of the inornate group roughly parallels the one of the intermediate group whereas the size increase in the ornate group seems to lag behind from the beginning. This probably reflects the tendency of the latter group to add relatively small chambers in this early ontogenetic phase. In the later stages the curve of the inornate group no longer remains so close to the one of the intermediate group but is seen to gain a larger distance. Apparently the inornate group of specimens cannot keep up with the rate of size increase set by the intermediate group and in the later phases it even tends to lose its lead on the ornate group of specimens.

For combinations of parameters O_i, A_i, E_i and k_i correlation coefficients were not calculated for the groups separately. For the inornate group of specimens in particular such r values would be based on small numbers of observations only and, moreover, differences were not expected to be present.

VI.4 CONCLUSIONS

Morphometric analysis of *Cycloclypeus* specimens from Ramla, Israel suggests that the embryon comprises the protoconch, the deuteroconch as well as the third chamber, which chamber was previously regarded as the first of the nepionic chambers.

In the subsequent nepionic part of the test two growth phases are recognized. The early one is characterized by relatively large growth steps and a waning degree of embracement of the chambers. In the later phase growth steps are markedly smaller and tend to decrease even further with increasing age, while the degree of embracement shows a fairly regular increase. On average this second phase begins with the formation of the seventh chamber.

At any nepionic stage i the size of the test depended on the initial size, i.e. the size of the embryon, and the rate of size increase. A large test-size at stage i is related to a high degree of embracement of the chamber built at this stage. Therefore large specimens reached the stage of cyclic growth in a small number of steps. As a result a large size at stage i or a high rate of size increase are not associated with a large precyclic stage.

In an earlier chapter it was shown that specimens with a large number of precyclic growth steps tend to have a large precyclic stage. However, this does not signify that the size of the precyclic stage is determined by the number of growth steps, as larger growth steps do not lead to a larger precyclic size but,

in fact, to a reduction in the total number of precyclic growth steps. It is therefore concluded that cyclic growth was achieved as some critical size of the test was reached and that a large critical size was on average reached in a larger number of growth steps. It is furthermore concluded that, more in general, in the later part of the nepionic stage the degree of embracement of the chambers largely depended on the size of the test.

At any nepionic stage i specimens showing a modest ornamentation were on average larger and showed larger growth rates than more ornamented as well as less ornamented specimens.

Chapter VII

MORPHOLOGICAL VARIATION AND DEPTH

In this chapter relations are discussed beteen depth of habitat and the internal and external morphology of *Cycloclypeus*. For a better understanding we will also review data and speculations on several other groups of larger foraminifera.

VII.1 EXTERNAL MORPHOLOGY

The ornaments on the test of Recent *Cycloclypeus* consist of imperforate, 'glassy' calcite. In our fossil assemblages they may be milky-white but this is probably due to recrystallization. Carpenter (1856) already noticed that the transparency of the ornaments contrasts strikingly with the 'semi-opacity' of the surrounding wall. In *Cycloclypeus* and in other genera of the Nummulitidae the transparent sculptural elements are thought to enhance light penetration (e.g. Drooger,1983). This would help to fulfil the light requirements of the algal symbionts usually present in the internal protoplasm of larger foraminifera. This explanation is supported by the better developed ornamentation in those representatives of Recent *Operculina* and *Heterostegina* that live in the deeper parts of the photic zone where light penetration is reduced (Hottinger, 1977a,b).

In our opinion, the variation in sculptural relief of our Oligocene Cycloclypei is explained best in the same way. On average the specimens of our intermediate morphogroups would thus derive from populations that lived in the middle part of the depth-range and inornate and ornate specimens would have lived in the upper and lower parts of this range, respectively. In his paper on *Cycloclypeus* from Borneo Drooger (1955) argued that thick-walled specimens lived in more turbulent waters than specimens with thinner walls. Our inornate morphotypes tend to be thicker than the more ornate ones in a rather restricted number of samples only. Yet, if test thickness has a link with water turbulence in our Mediterranean Cycloclypei as well, this observation still lends some support to the allocation of the inornate morphogroups to the upper parts of the depth-range.

If the differences in the internal morphology for our three morphogroups are thus linked to depth of habitat, the relation between depth and inner morphology seems to be quite different for the two areas we studied (Europe and Israel). We might try to reconcile these diverging results by supposing that the European samples contain *Cycloclypeus* specimens from the upper and middle

parts of the depth range only, whereas the Ramla assemblages would be constituted by specimens that lived in the upper and middle as well as lower parts of this range.

This creates, however, a new problem. As the range of variation in external morphology is only slightly larger in the Ramla locality with respect to the other sites, we would have to conclude that nearly the same range of sculptural variation was established in Europe in a considerably smaller depth interval. This would suggest a regional difference in the rate at which the sculptural relief increased with increasing depths.

Moreover, our attempt to fit the depth linked changes in internal morphology of both areas to a single pattern would still not be successful. From the European data we concluded that at each embryon-size level ornamented Cycloclypei have fewer precyclic chambers and convolutions than the inornate specimens from overall shallower habitats. We argued that this is probably connected with the overall smaller size of the precyclic stage in the ornamented specimens. Such differences were not observed in the assemblages from Ramla.

So, the differences in the results from both areas studied are not readily reasoned away. We think that more justice is done to the data if we accept that our Cycloclypei from Europe and Israel occupied more or less corresponding depth intervals and that the depth linked changes in internal morphology were truly different in both regions considered.

VII.2 EMBRYON-SIZE

Several other groups of larger foraminifera have been the subject of speculations on the response of internal morphological features to environmental factors. Attention is usually focussed on the relation between embryon-size and depth of habitat. In this section the results of these studies will be briefly, but critically reviewed for a comparison with our results on *Cycloclypeus*.

VII.2.1 Miogypsina

Drooger and Raju (1973) suggested that embryon-size in *Miogypsina* species reached larger values at higher latitudes. If this increase would be related to decreasing light intensity, local trends of increasing embryon-size with greater water depth were expected as well.

In the low-latitude assemblages of the *Cycloclypeus koolhoveni* lineage from Indonesia mean embryon-size is not smaller but larger than in the roughly corresponding assemblages of the *droogeri* lineage from higher latitudes in Europe. However, since we are not comparing assemblages from the same region, as in the case of the Miogypsinidae, the morphological differences for these Indone-

sian and European Cycloclypei may very well be related to other factors than depth. Therefore a local trend in embryon-size, induced by lower light intensity levels at greater depths, may still be valid for our Cycloclypei from Europe.

VII.2.2 Heterostegina

Fermont (1977b) and Biekart et al. (1985) studied assemblages of Recent *Heterostegina depressa* from successive depth levels in the Gulf of Elat and near Hawaii, respectively. Fermont reported an increase in embryon-size for *Heterostegina* from Elat down to a depth of approximately 80 metres but, as the author stated, an erratic picture of again lower values was found at greater depth (fig. 54). Also in the Hawaiian *Heterostegina* the size of the protoconch was shown to increase with depth in the 1 - 55 m interval investigated (fig. 55). A similar study by Bor (int.rep.), one of Biekart's co-authors, on Hawaiian samples extending to some 100 m of water depth showed no reversal to smaller sized embryons in these deeper samples. This pattern therefore shows resemblance to the one suggested for the Miogypsinidae by Drooger and Raju (op.cit.) but Biekart et al. did not consider light intensity as the controlling factor for the increase in embryon-size in *Heterostegina*. They suggested that the

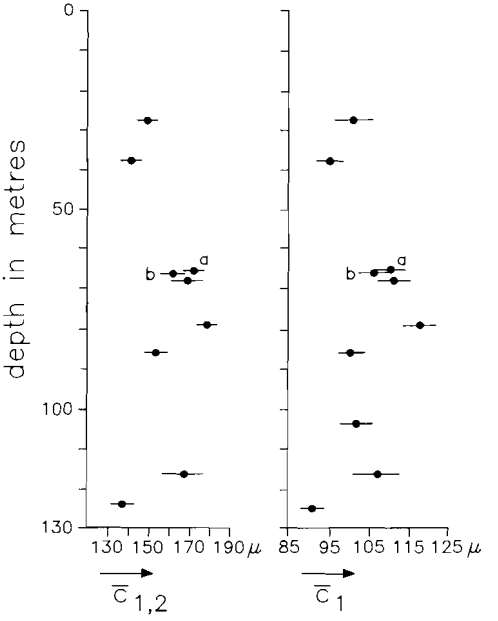

Figure 54: Depth plot of mean values (± 1 SE) of two parameters measuring embryon-size in *Heterostegina depressa* from Elat (after Fermont, 1977b).

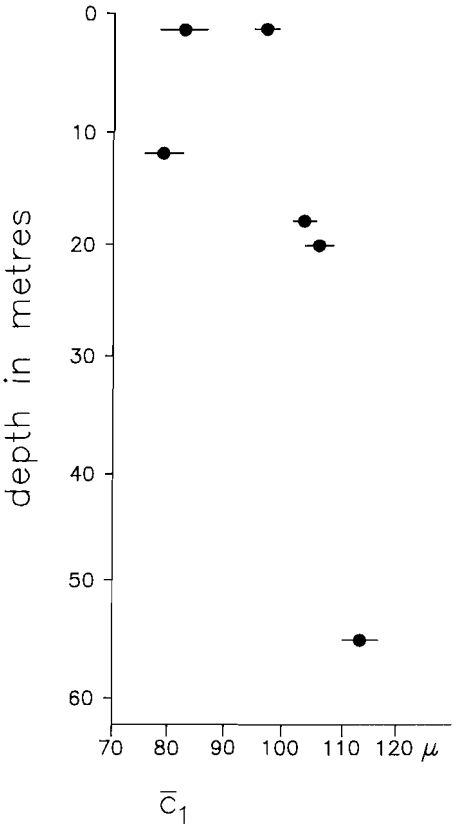

Figure 55: Depth plot of mean protoconch-size (± 1 SE) in *Heterostegina depressa* from Hawaii (after Biekart et al., 1985).

cline could be the result of changing proportions in the mixture of two types of megalospheres, which types possibly differ in mode of reproduction (fig. 56). According to Röttger et al. (1986) these types would even represent two different *Heterostegina* species but this hypothesis has been rejected in a more recent paper (Röttger et al., 1990).

The near absence of microspheric individuals in shallow waters near Hawaii suggests that sexual reproduction predominantly occurs in deeper water. Hottinger (1977b) reported that also in the Gulf of Elat the relative numbers of microspheric *Heterostegina* increase with depth and reach a maximum in the 60-70 m interval. Near this level relatively large mean embryon-size values for the megalospheres were recorded by Fermont (op.cit.) but this author did not distinguish more than one megalospheric type. However, two types of

megalospheric *Heterostegina* may still be present if it is assumed that their morphological differences are too small to be recognized in the depth assemblages. Also in the case of the Hawaiian *Heterostegina* the differences for both types were primarily discovered in laboratory cultures and only then the types could be traced in the sediment samples. So, a changing mixture of two types of megalospheres with depth could well be possible for the Elat data as well.

Some comment on the report by Biekart et al. is due, because the matter is more complicated than our short review is suggesting. The two types of megalosperes were called A_a and A_d. Type A_a has a megalospheric parent and/or produced megalospheres; type A_d has a microspheric parent and/or produced gametes. The morphological differences for both types were described from two A_a clones and four A_d clones only. The parent individuals of both

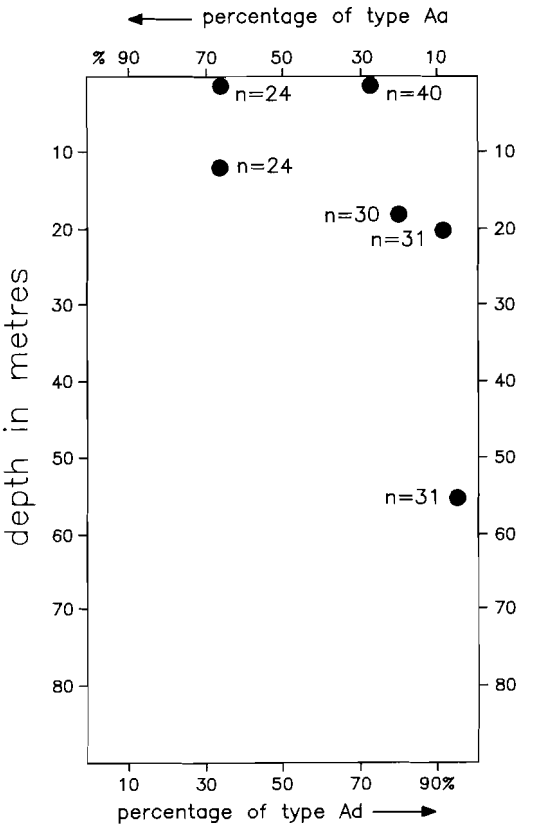

Figure 56: Ratio of the A_a and A_d types of *Heterostegina depressa* specimens in the depth samples from Hawaii (Biekart et al., 1985)

types of clones were harvested from different depth intervals: The two parents of the A_a clones from 1 and 10 m and the four parents of the A_d clones from 35 to 50 m. The specimens were raised under identical laboratory conditions but the recorded morphological differences may well relate to the difference in the original habitat of the parents in addition to a difference in mode of reproduction. In fact, another A_a sample was available from a parent, collected at a depth of 73 m and this clone, with large sized embryons, showed a morphology which was considered to be more characteristic of the other megalospheric type, A_d. This suggests that the results from the laboratory samples may have been seriously affected by the collection depth of the parents.

If the data on the 73 m sample are included in the discussion, the results seem to indicate that in the A_a type specimens embryon-size might be larger at greater depth. This would imply that a possible shift in the relative abundance of the two types in the depth assemblages does not adequately explain the cline recorded in the sediment samples, as a similar cline would already be present in the A_a types.

The embryon-size pattern of our European Cycloclypei resembles that of Hawaiian *Heterostegina*, whereas the pattern recorded in Ramla reminds us of the Elat data, where embryon-size seems to decrease at greater depth. Only single clusters of megalospheric *Cycloclypeus* can be distinguished in our Oligocene samples but it remains possible that actually two types are present. If such types differed in a similar way in mode of reproduction and internal morphology, the cline in embryon-size in our European Cycloclypei might be explained by changing ratios of two such types in successive depth populations.

Only 14 microspheric individuals of all the Cycloclypei investigated on inner and outer morphology could be assigned to one of our three morphogroups. As these data are small in number and not really clustering in any of these groups, they do not provide evidence for the assumption of depth related shifts in the mode of reproduction in our Oligocene *Cycloclypeus*.

No proof is available to accept or reject the possibility that differences in embryon-size for our morphogroups are due to a shift in the relative abundance of two biologically different types of megalospheres in successive depth assemblages.

VII.2.3 Operculina

Fermont (1977a) also studied the assemblages of *Operculina ammonoides* in his depth profile from Elat. He distinguished two types of specimens on external morphology: type 1 being evolute and flat and type 2 involute and thick.

The few observations on the involute group showed that mean protoconch-size values were larger in deeper samples but we agree with the author that this result may well have been accidental.

In one of the samples the evolute group of specimens could be subdivided into two types: small specimens with a relatively large protoconch (type 1a) and large specimens with smaller protoconchal chambers (type 1b). Fermont selected samples which were thought to be largely constituted of type 1a specimens. Their mean protoconch-size was shown to increase down to 79 meter of water depth and seemed to remain fairly constant further down to the level of the deepest of his samples at 130 meter (fig. 57). Fermont suggested that protoconch-size in the other type of evolute specimens (type 1b) remains relatively small throughout the entire depth interval studied.

If the data on all evolute specimens were lumped (type 1a + type 1b), mean protoconch-size was seen to increase with depth, reaching large values in the 70 to 90 m interval (fig. 58). In the deeper samples, however, a reversed trend was observed down to the deepest level sampled at 150 m with only one excep-

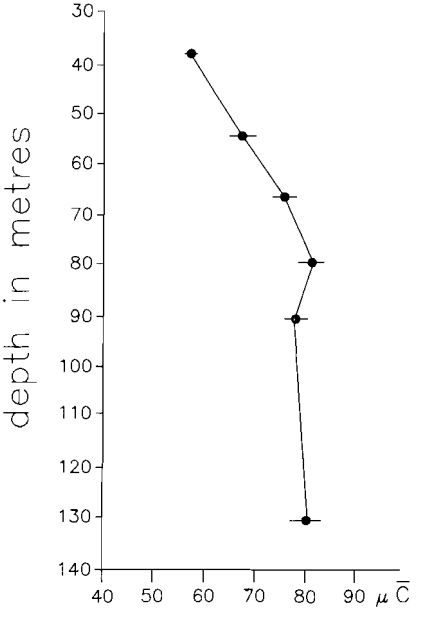

Figure 57: Relation between depth and mean diameter of the protoconch (± 1 SE) in type 1a specimens of *Operculina ammonoides* in Elat (Fermont, 1977a).

tionally large value in the 130 m sample. From this pattern Fermont inferred that the assemblages from the middle part of the depth range were dominated by type 1a specimens with their larger embryons and those from the upper and lower parts by type 1b specimens with invariably small embryons.

In view of the results on *Heterostegina depressa* from Hawaii we might suppose that the two types of evolute *Operculina* in Elat differ in their mode of reproduction. Type 1a specimens would then probably reproduce sexually and an asexual mode of reproduction would predominate in type 1b with its small embryons. This would concur with the maximum relative frequencies of microspheric *Operculina* specimens in the 80 to 100 m depth interval and their near-absence between 30 and 50 m of water depth in Elat as recorded by Hottinger (1977b). This concept provides some kind of explanation for the trend

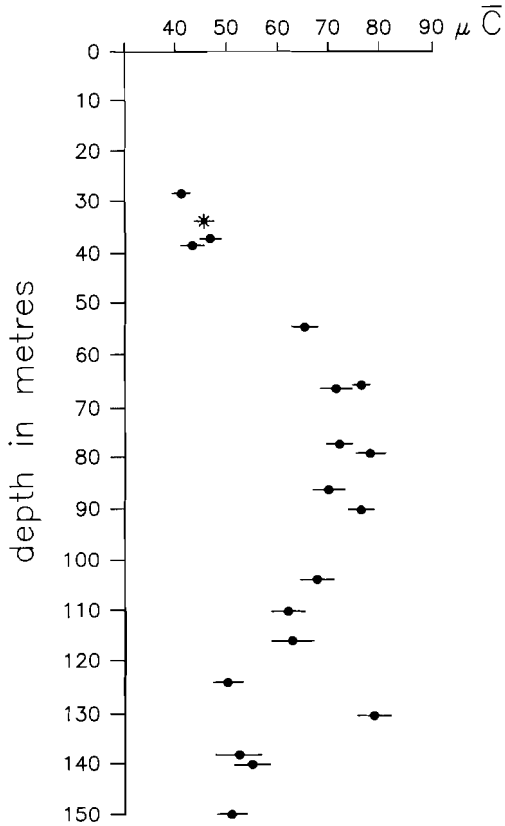

Figure 58: Relation between depth and mean diameter of the protoconch (± 1 SE) in type 1a and type 1b specimens together of *Operculina ammonoides* in Elat (after Fermont, 1977a).

towards lower protoconch-size values in the deepest part of the depth range of *Operculina* if sexual reproduction is really reduced to again lower levels in these deep habitats. But the depth related increase in protoconch-size in the upper and middle parts of this range cannot be explained by changing ratios of the two types only, as an increase would already occur in one of the two types considered (type 1a). Therefore, if the concept of Biekart et al. (op.cit.) is applied to *Operculina* from Elat, it apparently does not adequately explain the observed morphological changes with depth. As in the case of Hawaiian *Heterostegina*, at least a second mechanism seems to be involved, like e.g. the one suggested for the Miogypsinidae, accounting for the protoconch-size increase in one of the types.

In a later paper by Fermont et al. (1983) the distinction between the two types of evolute *Operculina* specimens in the suite of samples from Elat was no longer carried through. Mean protoconch-size of all evolute specimens was shown to be positively correlated with the number of specimens in one gram of dry residue (fig. 59) and both these parameters showed a negative correlation with $\delta^{18}O$ values. The authors concluded that the common factor in these relations is productivity. In the middle part of the depth range, where relatively large protoconch-sizes are recorded, the production of tests would be high as well as the photosynthetic activity of the algal symbionts. However, no effort was made to fit this concept to the earlier conclusions of Fermont (1977a).

If the depth related variation in embryon-size in evolute *Operculina* is, to a limited extent, due to a changing mixture of two types of megalospheres (Fermont, 1977a), we expect to find some relation between the relative abundance of these types in the depth samples and the level of productivity. We already supposed that these types differ in their mode of reproduction. We furthermore pointed out that in that case their relative frequencies in the samples can be explained by the depth related change in the mode of reproduction which is indicated by the distribution of the microspheric specimens. The link with productivity might be looked for in the optimum environmental conditions which are thought to prevail in the middle part of the depth range with its high levels of productivity.

Hottinger (1977b) supposed that only under such favourable conditions sexual reproduction occurs in Recent *Operculina* (and *Heterostegina*), whereas reproduction would proceed asexually in the marginal zones of the distributional area. Although this line of reasoning seems to be consistent with the data available, we prefer to tackle the problem from a different angle, starting with the data on the numbers of specimens per gram of residue. These were interpreted in terms of productivity by Fermont et al. but we might as well substitute population-density for productivity.

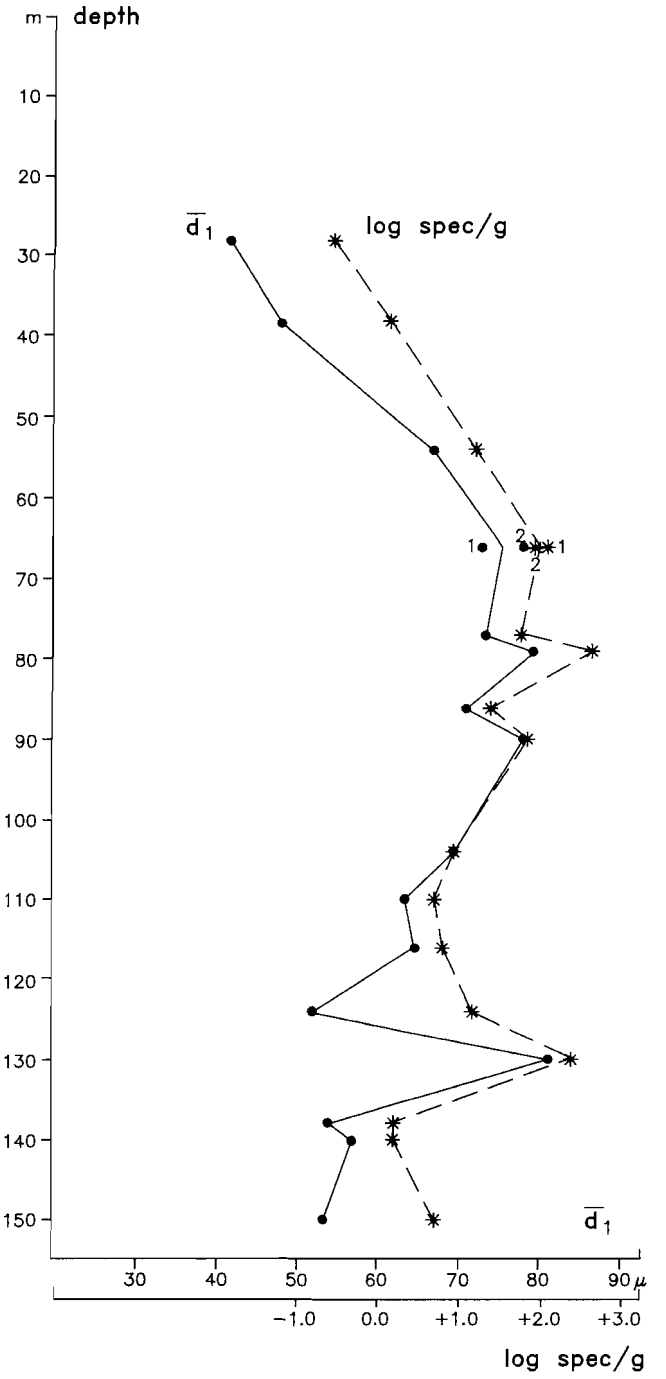

Figure 59: Depth distributions of the mean diameter of the protoconch in type 1a and type 1b specimens together and of the number of these evolute *Operculina ammonoides* specimens in one gram of dry residue (data Fermont et al., 1983).

Microspheric specimens are thought to result from the fusion of two gametes, which are released by megalospheres. The release of gametes was only sporadically observed under laboratory conditions, in cultures of *Heterostegina depressa* (Röttger & Schmaljohann, 1976). However, no microspheric specimens are generated, which probably requires, as already supposed by these authors, the presence of gametes from at least two different parents. They furthermore reported that these gametes are small (approximately 3 μ), short-lived and subject to predation, even in the culture dishes.

We therefore expect that in the natural environment of *Heterostegina*, or in that of other larger foraminifera, success in sexual reproduction is generally related to population-density. In high density populations the chance for two gametes to meet is increased and the hazardous time-lapse between release by the parents and fusion of the gametes is reduced.

Even if sexual reproduction in e.g. *Operculina* would occur throughout its depth range, the relative number of microspheres, which are the result of successful sexual reproduction, would be very small in marginal, low-density populations, whereas it would be larger in intervals occupied by larger numbers of specimens.

The remaining part of the variation in embryon-size with depth in *Operculina* Fermont (1977a) ascribed to changes occurring in his 1a type specimens. As described earlier this change was inferred from mean protoconch-size values of selected depth samples, which largely contained this type of specimens. However, also these values are correlated with the $\delta^{18}O$ values and the numbers of specimens per gram of residue, which data were provided by Fermont et al. (1983). Therefore also this part of the variation seems to be related to productivity.

In view of these correlations we expect a reversed trend towards smaller protoconch diameters in the deepest part of the depth range in this group of 1a specimens. The resulting pattern would therefore resemble the one recorded for all evolute specimens together. Fermont (1977a) could not document such a reversal in the deep samples but the stability in protoconch-size which was thought to characterize this depth interval instead, was inferred from the data on one sample only. The other samples in this interval were judged to be unfit for the reconstruction of any depth cline. The one sample that did qualify, was the one from 130 meter water depth with its exceptional values for the parameters indicative of productivity. Also for its large mean protoconch-size it bears more resemblance to the samples from the assumedly most productive middle part of the depth range than to those from the overall low productive deep part. So it seems that the 130 m depth sample is not representative for this group of deep samples and we think it is therefore rather unfortunate that Fer-

mont based his reconstruction of the lower part of the depth cline in the group of type 1a specimens on this sample only. We suggest that mean protoconch-size in this group shows a trend towards smaller values in most of these deep samples parallel to the trend in productivity as indicated by the $\delta^{18}O$ values and the numbers of specimens per gram of residue.

In the mean protoconch-diameter of the other group of evolute *Operculina* (type 1b) no obvious cline with depth was observed by Fermont. From this the remarkable conclusion might be drawn that protoconch-size in these specimens is not related to productivity and that therefore such a relation would exist in the 1a-type specimens only. However, such a conclusion should be considered with some caution. Only two samples, the uppermost and lowermost ones, were estimated to be largely constituted by these type 1b specimens, which would be practically absent in the middle part of the depth range. If the occurrence of this type is therefore mainly confined to the asssumedly low productive marginal zones of the depth range, the low embryon-size estimates for the few samples concerned could still be in accordance with a relation between embryon-size and productivity. Anyway, in our opinion the possibility that such a correlation is valid for both types of megalospheres, cannot be rejected.

Drooger (1983) tried to understand the link between large embryon-size and high levels of productivity in *Operculina* by supposing that the inferred optimum environmental conditions, prevailing in the depth interval concerned, would allow specimens to grow to large sizes. Therefore also the daughter individuals, resulting from the asexual reproduction of these large parents, would start life with an increased volume of protoplasm.

As, however, reported earlier (Laagland,1988) the situation is probably not this simple. Drooger assumed that the number of offspring is not related to the size of the parent, whereas observations by Röttger (1974) and Hallock (1985) indicate that the numbers of juveniles are larger for parent individuals of larger size. To explain the correlation between distributional frequencies (productivity) and embryon-size in *Operculina* I alternatively suggested (Laagland,op.cit.) that near the upper and lower ends of the depth range the number of offspring in asexual reproduction is increased at the expense of embryon-size. This can then be understoood as an effort to compensate for the overall lower numbers of specimens produced by the low-density populations living in these (sub-)marginal zones of the distributional area.

The depth cline in embryon-size, reconstructed for *Cycloclypeus* from Ramla, seems to show a pattern which resembles the one in the evolute *Operculina* from Elat. The suggested mechanisms at work in *Operculina* may therefore have operated in the case of the Ramla Cycloclypei as well. The possibility can-

not be rejected, however, that two types of megalospheres, which differ in their mode of reproduction, are present in the Israelian assemblages. Although not a single microspheric specimen was observed in our ample material from the Ramla locality, this hypothesis remains hard to falsify. Anyway, if two types are present, both are thought to show the same type of depth related variation in mean embryon-size, with larger values in the middle part of the depth range. With reference to the case of *Operculina* this would imply that Oligocene *Cycloclypeus* from Israel reached high production levels and high distributional frequencies in the mid-depth trajectory. Such a distributional pattern seems to be quite feasible and is not contradicted by the relative abundances of our morphotypes in the Ramla assemblages. Moreover, our analysis of the k_i values in the previous chapter revealed that the specimens, which would have lived at intermediate depths, tend to show overall higher rates of test-size increase than other specimens. This may indicate that in Ramla relatively high production levels were indeed reached in some middle part of the depth range.

VII.2.4 Discocyclina

Finally we wish to mention an Eocene example of a depth related cline, which was again provided by Fermont (1982). For the *Discocyclina varians* group in the Ein Avedat deposits from Israel he concluded that extremely flat specimens were deep-living; they have a small embryon. In most samples a continuous variation is present from these *D. augustae* morphotypes to *D. varians* morphotypes, which are thicker and presumably lived in shallower parts of the depth range. The shallowest of these populations would have had smaller embryons than the populations at intermediate depths. The clinal variation in mean embryon-size in this *D. varians* group resembles that of evolute *Operculina* from Elat and that of our *Cycloclypeus* from Ramla. Fermont (op.cit.) suggested that in marginal zones of a species' (depth-) distribution specimens must be less specialized and that embryon-size is some kind of measure for the degree of specialization. However, we suggest that embryon-size in these Eocene discocyclinids was related to the supposedly bell-shaped frequency distribution of this group with depth.

VII.2.5 The two patterns

From our review it appears that the clines in *Operculina* and *Discocyclina* as well as the one in *Cycloclypeus* from Ramla show corresponding patterns. These clines in embryon-size may be explained by differences in population-density, which probably correspond to depth related changes in environmental conditions. The link between population-density and mean embryon-size may be

twofold. Two types of megalospheres may be involved, which differ in embryon-size and mode of reproduction. Population-density, with its inferred influence on success in sexual reproduction, could, at least to some extent, determine the relative abundance of the two megalospheric types in each depth population and consequently, the population's mean embryon-size. Secondly, if two types are present, both are thought to show a relation between embryon-size and population-density, which possibly results from changes in the numbers of juveniles produced by a single parent during asexual reproduction.

A second pattern seems to be present in *Heterostegina* from Hawaii, *Cycloclypeus* from Europe and, less distinctly so, in *Heterostegina* from Elat. In these cases no distinct reversal could be documented towards smaller embryons in the deep part of the investigated depth-ranges. A similar pattern of increasing embryon-size with depth was inferred for *Miogypsina*.

Difficulties arise when we try to explain both clinal patterns in similar terms. With some difficulty the data on the deep *Heterostegina* assemblages from Elat may still fit an overall decrease in mean embryon-size. But this cannot be claimed anymore for the Hawaiian data. On the basis of the data on protoconch-diameter we might suppose that *Heterostegina* is still abundant in deep waters around Hawaii (down to at least 100 m). No frequency data are available but in our view such a distribution seems hardly probable.

In European *Cycloclypeus* the small differences in mean embryon-size for our three groups would signify that depth related differences in population-density were correspondingly small. This at least, seems to be in accordance with the extremely low relative frequencies of the genus in our residues. We are quite confident that *Cycloclypeus* was nowhere abundant in the European region, which fact indeed would have reduced the density gradient along any local depth profile.

So, the small values for the differences in embryon-size for the morphogroups in our European samples may still be consistent with an explanation in terms of population-densities. Yet, the apparent sustained increase in embryon-size with depth would imply that the genus was more abundant towards greater depth, down to its lower depth limit. The lower end of the depth distribution would have shown an abrupt break which might have corresponded to a similar break in some environmental parameter, such as for instance the type of substrate.

In the Gulf of Elat such a break is illustrated by the lower depth limit of the vegetated area at approximately 80 metres. But this lower limit of the *Halophila* meadows does not induce a conspicuous change in the depth distribution of *Heterostegina* or *Heterocyclina*, which are both closely related to *Cycloclypeus*. In *Operculina* the break in the type of substrate may be merely reflected by a

change in the relative abundance of the evolute and involute types in the assemblages (Fermont et al.,1983). On the other hand we might suppose that the lower depth limit of European *Cycloclypeus* coincided with an abrupt change in the depth profile, which for instance might have corresponded to a transition from shelf to slope environment. But we would still feel uncomfortable, for instance because the relative frequencies of the morphotypes in our assemblages do not reflect the inferred quantitative distribution of the genus with its supposedly increasing numbers at greater depth. In most of our European assemblages the highest relative frequencies are recorded for our intermediate morphotypes but this is no decisive argument, among others because these frequencies depend on the arbitrarily set limits between the morphogroups.

We are, therefore, forced to admit that the clinal pattern in European *Cycloclypeus* may still result from depth related differences in population-density. But we have the impression that our approach is too simplistic and that it does not explain the peculiarities in this case or in that of Hawaiian *Heterostegina* in an elegant way.

VII.2.6 Light intensity versus population density

The pattern of sustained embryon-size increase with depth in Hawaiian *Heterostegina* or European *Cycloclypeus* might alternatively originate from the concomitant decrease in light intensity, as suggested by Drooger and Raju (1973) in the case of *Miogypsina*. It may well be that under the lower light intensities at deeper levels, larger numbers of symbionts are necessary to support the life activities of the host. As these symbionts are evenly distributed over the daughter cells during asexual reproduction, the number of progeny could show a tendency to decrease with depth, allowing for an increase in the number of symbionts and the embryonic size of single daughter cells.

The concept of Drooger and Raju may also be reconciled with the one of Biekart et al. (1985), if we assume that the changing ratios of the two types of megalospheres, in the case of Hawaiian *Heterostegina*, reflect a relative increase in sexual reproduction with depth as a function of decreasing light intensity. Yet, we wish to refrain from further speculative reasoning, which only served to illustrate that in our opinion the concept of Drooger and Raju is quite reasonable and may help to understand the apparently conflicting results of studies on clinal variation in larger foraminifera.

At this point we would like to present a model for depth clines in embryon-size, particularly for Oligocene *Cycloclypeus*. Other models may be formulated but, in our opinion, the following one fits the scanty data best.

Basically, clines in embryon-size would consist of a sustained increase with increasing depth. This increase in embryon-size would be modest, independent of density differences in populations along the depth profile and in some way dependent on the concomitant decrease in light intensity. The number of algal symbionts required to sustain the animals' life activities, may be the crucial link. In European *Cycloclypeus* it is this part of the model that would have been effective.

Secondly, this pattern of sustained embryon-size increase with depth may be modified by large density differences in populations of successive depth levels. As outlined earlier, sexual reproduction is expected to be more successful in high-density populations. This effect may contribute to an increased proportion of megalospheres from the micospheric generation and, consequently, to increased overall mean embryon-size values. Alternatively, or additionally, in asexual reproduction the number of offspring from a single parent may increase in low-density populations at both ends of the depth range. The initial size of the daughter individuals would be reduced in favour of an increase in the low numbers of specimens produced in such marginal populations

Thus, in a species which is very abundant in some middle part of its depth range (showing a bell-shaped frequency distribution with depth) embryon-size may show the following changes with increasing depth. The light-induced increase in embryon-size is initially reinforced by the effect of increasing population-density down to some depth level beyond which the reversed effect of decreasing densities will counteract the continued trend toward larger embryons in response to waning light intensity. This may result in overall decreasing embryon-size values in the lower part of the depth range.

This density-induced modification of an originally sustained embryon-size increase with depth is thought to apply to our Ramla Cycloclypei in particular. Density differences in this abundant group are inferred to have been much larger than those in the rare *Cycloclypeus* from Europe.

VII.3 SIZE AND SHAPE OF THE NEPIONIC STAGE

Among the enumerated groups of larger foraminifera which would show depth related changes in internal morphology, a delimited nepionic stage is observed only in *Miogypsina, Discocyclina* and *Cycloclypeus*. On the depth cline suggested for *Miogypsina* (Drooger & Raju,1973) no nepionic data are as yet available and Fermont found no relation in his *Discocyclina varians* group between nepionic characters and estimated depth of habitat. The discussion is therefore necessarily restricted to the Oligocene Cycloclypei.

Apparently, the nepionic morphology of our Cycloclypei changed from

shallow to deeper parts of the photic zone. According to the European data the number of nepionic chambers and the number of convolutions tend to become reduced in specimens from deeper habitats. In Ramla such a trend with depth was restricted to the upper part of the depth range and it is apparent in parameter X. In the lower part of the depth range a reversed trend occurred as illustrated by a significant reduction in parameter γ.

We already noted that these changes in parameters X and γ are to some extent related to concurrent changes in embryon-size. Starting from a larger embryonic size a reduced number of growth steps seems to be sufficient to reach the size at which cyclical growth is achieved. In our opinion, the depth related changes in the nepionic configuration of the Cycloclypei from Ramla may well be considered in this way. Here the changes in the embryon dimensions are more distinct than those in the nepionic parameters.

The rate of growth may be another factor attributing to the changes in nepionic morphology. Relatively high growth rates were recorded for Ramla specimens with intermediate ornamentation. As this generally tends to reduce the number of nepionic growth steps, this effect is thought to reinforce the changes in nepionic morphology induced by the depth related changes in embryon-size. The low average numbers of precyclic chambers and convolutions, which probably characterized the Ramla assemblages from intermediate depth levels, would have been induced by relatively large mean embryon dimensions and to a limited extent by relatively high average growth rates.

For the European Cycloclypei an effect caused by differences in growth rates, could not be established as relevant data are not available. The depth related change in embryon-size is furthermore small. Its effect on the nepionic configuration therefore seems to be restricted. Yet, the changes in the nepiont are more distinct than in the Ramla Cycloclypei. This is probably connected with the overall reduction in size of the nepiont in deeper parts of the depth range as suggested by our data on parameter D_X. Such a trend could not be recognized in the Ramla data. This reduction in nepionic size probably induced a reduction in the number of nepionic growth steps (cf. X). The depth related reduction in the number of convolutions is less distinct and seems to be a secondary effect, as a smaller number of spiral chambers can be accommodated in a smaller number of convolutions.

So, in our opinion the depth related reduction in the number of nepionic chambers and convolutions in European *Cycloclypeus* is mainly determined by a reduction in the size of the precyclic stage. As in our assemblages parameter D_X is more closely related to parameter X than to parameter γ, the change in X is more distinct than the one in γ. The opposite would be expected if the

changes in X and γ were mainly determined by the concurrent change in embryon-size, as in the assemblages embryon-size is more closely linked to parameter γ than to parameter X.

The depth related changes in parameters X, γ and D_X in these European Cycloclypei strongly resemble similar changes in the course of evolution, as documented for instance for the *droogeri* lineage. The relation between these trends will be discussed in chapter XI.

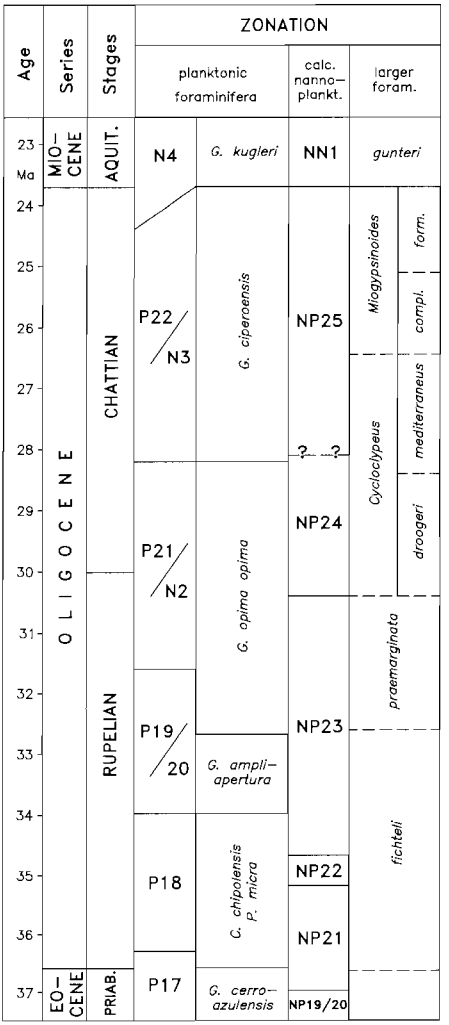

Figure 60: Biostratigraphic scheme (revised after Drooger & Laagland, 1986).

Chapter VIII

BIOSTRATIGRAPHY

VIII.1 CONCLUSIONS

Our biostratigraphic conclusions are summarized in figure 60. Some differences are apparent with the earlier concepts of Drooger and Laagland (1986). This partly results from our choice to abandon the zonal scheme of Hardenbol and Berggren (1978) and to adopt the more recent one of Berggren et al. (1985), instead of considering both options at the time as in Drooger and Laagland.

Most importantly, the *praemarginata* Zone is placed in the lower part of the Oligocene (Rupelian) instead of the upper part (Chattian). The Lower Oligocene now contains the *fichteli* and *praemarginata* Zones as well as the basal part of the *Cycloclypeus* Zone. The Upper Oligocene contains the larger part of the *Cycloclypeus* Zone and the *Miogypsinoides* Zone. The base of the *Cycloclypeus* Zone is now correlated with some level near the NP23-NP24 zonal boundary (e.g. SP724, Villajoyosa). The base of the *praemarginata* Zone is thought to correspond to some level in the basal part of Bolli's *G. opima opima* Range Zone (data de Mulder,1975).

There are no indications in our correlations for a conspicuously heterochronous (non-synchronous) character of the nepionic evolution in the *C. droogeri* lineage within the Mediterranean region. Therefore, the distinction of the *C. droogeri* and *C. mediterraneus* Subzones is thought to be useful for biostratigraphic purposes. This is less clear for the distinction of the *M. complanata* and *M. formosensis* Subzones. In the basal part of the *Miogypsinoides* Zone invariably primitive assemblages of *M. complanata* are recorded and in the top part assemblages occur of the more highly developed species of *M. formosensis* and *M. bantamensis*. However, as these levels are probably separated by a gap in our sample record, the evolutionary history of these European miogypsinids is still ill-documented within this time-interval.

Chapter IX

SPECIES-RELATIONSHIPS IN CYCLOCLYPEUS

In this chapter we will briefly recall the main characteristics of the Oligocene *Cycloclypeus* species and offer suggestions on their relationships.

IX.1 THE SPECIES OF THE DROOGERI LINEAGE

The two species of the Mediterranean *droogeri* lineage are of course closely related as *C. mediterraneus* directly descended from *C. droogeri*. In both species the sculptural elements on the surface of the test generally show a variety of shapes, ranging from raised sutures and drop-like structures to blunt and broad pustules.

The *mediterraneus* assemblages from Ramla are slightly different from the Spanish and Italian ones. The Ramla Cycloclypei tend to show larger embryons and relatively small numbers of precyclic chambers and convolutions with respect to the dimensions of their precyclic stage. On external appearance the Ramla specimens may show more elevated and less expanded sculptural elements than the specimens in the other assemblages. These differences in internal and external morphology may well relate to the rather remote position of the Ramla area with respect to the other two Mediterranean regions.

VII.2 CYCLOCLYPEUS KOOLHOVENI

The Cycloclypei of the Indonesian *koolhoveni* lineage differ from those of the Mediterranean *droogeri* lineage in their overall larger embryon dimensions and particularly in the large size of the deuteroconch with respect to the size of the protoconch. The nepionic whorls show a very rapid increase in height compared to all other *Cycloclypeus* species (Tan, 1932; our plate 6). As more nepionic chambers can be accommodated in these spacious whorls, relatively small numbers of convolutions (γ) are observed in the *koolhoveni* specimens.

Inspection of Tan's plates and of specimens from the type locality of Tjimanggoe (Java) strongly suggests that primitive *koolhoveni* specimens have a larger precyclic stage than primitive *droogeri* specimens with corresponding numbers of precyclic chambers. The nepionic stage of the primitive *koolhoveni* specimens figured by Tan were measured by O'Herne (1972). According to this author the approximate dimensions of this stage are 5.2 × 3.7 mm. In our most primitive *droogeri* assemblage the nepionic stage is indeed smaller, judging from the mean nepionic diameter values ($\bar{D}_X$) of 2.52 mm.

Advanced assemblages of the Mediterranean lineage show fewer precyclic chambers ($\bar{X}$ = 16.1) than advanced *koolhoveni* assemblages ($\bar{X}$ = 23.8)). In the Mediterranean lineage the reduction in size of the precyclic stage seems to be extended as well, because in addition to the smaller number of precyclic growth steps also initial (embryon-) size is smaller. In the *droogeri* lineage, therefore, evolution seems to have led to a higher level of nepionic development than in the *koolhoveni* lineage.

Also in external appearance the Cycloclypei of the *koolhoveni* lineage differ from those of the *droogeri* lineage. The Indonesian specimens tend to show a more delicate sculpture which may consist of more numerous and more elevated pustules. Pustules may furthermore be situated on the chamberlet-walls proper, next to the more frequent pustules overlying the septula. In general the Indonesian specimens seem to have a less inflated umbonal part and a thinner flange than the specimens of the *droogeri* lineage.

In spite of these differences in external and internal morphology the *koolhoveni* and *droogeri* lineages are thought to be related rather closely. A polyphyletic origin of the groups is thought unlikely. We support the conclusion of Tan (1932) that *C. koolhoveni* descended from a flat, evolute *Heterostegina* species. The primitive *koolhoveni* specimens of Tjimanggoe are accompanied by large, spirally arranged, *Heterostegina*-like specimens, which are otherwise identical to the *koolhoveni* specimens. For these spirally arranged specimens Tan erected the species names *Heterostegina praecursor* and *Heterostegina bantamensis*. The juvenile specimens in the association cannot be allocated to either the *Heterostegina*- or to the *Cycloclypeus*-group and thorough biometrical analysis of the juvenile stages failed to reveal any heterogeneity in embryon-size or in other features of the spirally arranged chambers (Kesseler, int.rep.). We therefore suggest that the *Heterostegina*- and *Cycloclypeus*-like morphotypes from the locality of Tjimanggoe constitute a single homogeneous assemblage of very primitive Cycloclypei in which the cyclic stage is reached by a restricted number of the specimens only.

Primitive *droogeri* assemblages from the vicinity of Villajoyosa (Spain) are accompanied by flat, evolute *Heterostegina* specimens as well. But these groups do not show such a close resemblance in their early ontogenetic stages. The *Heterostegina* specimens are recognized by their relatively irregular, coarse mesh-work of chamberlets when compared with the accompanying Cycloclypei. Similar *Heterostegina* assemblages occur at lower stratigraphic levels as well, where *C. droogeri* is not yet present (Geeraets, int.rep.).

We therefore suggest that after *Cycloclypeus* originated in the Indo-Pacific realm from a *Heterostegina* ancestor, some primitive stock migrated to the

Mediterranean region and gave rise to the *droogeri* lineage. *C. droogeri* and *C. koolhoveni* might be regarded as (sub-)species, which lived at about the same time in different bioprovinces, between which there was only limited genetic exchange, if at all. *C. mediterraneus* and *C. koolhoveni* might be regarded in the same way but we do not know whether the latter species did not become extinct prior to the ascent of the second Mediterranean species. Anyway, the *mediterraneus* assemblages from Ramla show several morphological traits which appear to be intermediate between the characteristics of the Spanish-Italian assemblages of the *droogeri* lineage on the one hand and of the Indonesian *koolhoveni* assemblages on the other. This nicely concurs with the equally intermediate position of the Ramla area from a geographical point of view.

IX.3 CYCLOCLYPEUS EIDAE

Cycloclypeus eidae is primarily characterized by its small embryon-size. In Indonesia it shows smaller mean numbers of precyclic chambers than advanced *C. koolhoveni*. In the Mediterranean region *eidae* assemblages of primitive build show larger mean numbers of such chambers than advanced *C. mediterraneus*. *C. eidae* has a small precyclic stage with respect to the number of precyclic chambers and convolutions. Compared to the Cycloclypei of the *droogeri* and *koolhoveni* lineages the *eidae* specimens tend to show a larger number of convolutions with respect to the number of precyclic chambers. This may be caused by a slow increase in the height of the whorls. In median sections *C. eidae* shows a fine and regular mesh-work of chamberlets compared to the coarse and more irregular build of the specimens in the *droogeri* and *koolhoveni* lineages (plates 6-9).

In external appearance *C. eidae* is conspicuously different from the species of the *droogeri* lineage. It is more delicate in its sculpture which is mainly constituted by numerous fine pustules. It furthermore tends to show a thinner flange and a less prominent central swelling. As *C. eidae* bears more resemblance in outer appearance to *C. koolhoveni* than to the species of the *droogeri* lineage, it is considered to be more closely related to the Indonesian lineage.

One might object that ornamentation in *Cycloclypeus* is susceptible to environmental circumstances and should therefore be considered of little taxonomic value. However, the differences in ornamentation for the species of the *droogeri* lineage and *C. eidae* are not easily explained by ecological differences. These species lived in the same Mediterranean region and the Mediterranean *eidae* specimens show a close resemblance to those reported from the Indo-Pacific region. Furthermore, we do not think that the habitat of *C. eidae* was

really that much different from the one occupied by *C. droogeri* or *C. mediterraneus* as was supposed by Drooger and Roelofsen (1982). Their suggestion was partly based on the incorrect assumption that, in contrast to the ornamented specimens of *C. eidae*, the Cycloclypei of the *droogeri* lineage were predominantly smooth.

We do support the assumption of these authors that *C. eidae* is an immigrant species in the Mediterranean region which probably originated somewhere in the Indo-Pacific realm. Although it seems to succeed *C. koolhoveni* in time, it is doubtful that *C. eidae* directly descended from this species. The two species are quite different in internal morphology and intermediate or mixed assemblages have not been recorded. As stated by Drooger and Roelofsen it might easily be imagined that some remote stock of Cycloclypei, occupying a peripheral position with respect to the main distributional area of *C. koolhoveni*, underwent a rapid process of evolutionary change. In the classical punctuation theory (Eldredge and Gould, 1972) the earlier mentioned selective advantages in the nepionic characters of *C. eidae* may have enabled a rapid increase in numbers after invasion of the main distributional area of the genus. If we assume that no significant gaps are present in the record, the absence of intermediate assemblages seems to rule out the possibility that the two stocks of Cycloclypei were capable of interbreeding.

If on the other hand the concept of bottleneck-frequencies in evolution (Drooger, 1984) is applied to the present case, an alternative and more attractive explanation may be offered. In that event the main *koolhoveni* stock may have dwindled in numbers in the first place or even became extinct, before *C. eidae* took over its former distributional area. This chain of events could easily explain the absence of mixed or intermediate assemblages. There is no need to assume a total genetic isolation of both stocks. Neither does this solution require a rapid decline in the frequencies of *C. koolhoveni* as a result of inferred selective disadvantages on account of its more primitive nepionic build. The initial reduction in numbers of the old stock may have been caused by an event, like some epidemic disease, which did not occur in the area occupied by *C. eidae* or did not affect this species at all.

In the Mediterranean region *C. eidae* succeeded *C. mediterraneus*. As mentioned earlier, the immigrant species shows a larger number of precyclic chambers than the advanced assemblages of the indigenous *C. mediterraneus*. Still, *C. eidae* is thought to be more advanced in nepionic evolution as the size of its precyclic stage is smaller than in the species it replaced.

The timing of this migrational event with respect to the first occurrence of *C. eidae* in the Indonesian region is difficult to establish. We have little control

of chronostratigraphic value. From the Indonesian sites data on planktonics are lacking and reliable determinations on accompanying larger foraminifera are available on the generic level only. In the Mediterranean region species of the subgenera *Eulepidina*, *Nephrolepidina* and *Miogypsinoides* are associated with advanced *C. mediterraneus* and with *C. eidae*. According to Tan's report the Indonesian assemblages of advanced *C. koolhoveni* and primitive *C. eidae* are associated with species of the two subgenera of *Lepidocyclina*. Only the higher developed *eidae* assemblages in this region are accompanied by representatives of the genus *Miogypsina*.

These data give the impression that in the Mediteranean region *C. eidae* entered the record later than in Indonesia. This impression is supported by the more advanced build of the replaced end-members of the *droogeri* lineage with respect to the more primitive level of nepionic development reached in the *koolhoveni* lineage.

From the data on the Mediterranean Cycloclypei it cannot be ascertained whether the immigration of *C. eidae* gave rise to mixed or hybrid assemblages. The two taxa concerned are quite different in internal as well as external morphology and therefore they are thought to be only remotely related. If they occurred together at all, genetic exchange between the two stocks of Cycloclypei is likely to have been negligible, if present at all. In that case *C. eidae* may have eliminated *C. mediterraneus* on account of its more advanced nepionic build. Alternatively, *C. eidae* may have invaded the area after it was vacated by *C. mediterraneus*.

IX.4 THE CARPENTERI-TYPES

Except for the difference in embryon-size and the corresponding difference in the number of precyclic chambers, similarities in the morphology of the *eidae*-types and *carpenteri*-types suggest that both types are closely related. Their joint occurrences in our assemblage from Granada, Spain, as well as in Indonesia, in assemblages from a considerable time interval, also seem to point in this direction. Following the hypothesis of Drooger (1955) the two types are thought to belong to a single species. The assemblages of this species are considered to be homogeneous although clearly bimodal distributions may be recorded in embryon-size and number of precyclic chambers. For such mixed assemblages Tan's species name *C. posteidae* might be used. However, we prefer the label of *C. eidae* as the mixing of the types is considered to be characteristic of the entire lineage.

It does not seem to be realistic to ascribe the bimodality in assemblages of this lineage to morphological differences between microspheric and

megalospheric individuals, as was suggested by Drooger (op.cit.). We suggest that the *eidae*-trait was a dominant hereditary character. In that case the *carpenteri*-morphology was phenotypically expressed only in haploids and homozygous megalospheric diploids, with respect to this trait. These would have slowly increased in numbers at the expense of *eidae*-haploids, megalospheric homozygous *eidae*-diploids and megalospheric heterozygous diploids, which would all have shown the *eidae*-morphology. To our knowledge there is, however, no evidence to support or reject this suggestion.

Chapter X

TEST-MORPHOLOGY OF CYCLOCLYPEUS IN SPACE AND TIME

In this chapter we will briefly recount the depth-related and geographical differences and the time-bound changes which are apparent in the morphology of *Cycloclypeus*. Three aspects of the test will be treated: Sculpture, embryon-size and nepionic morphology. Similarities in space-related and time-bound changes will be shortly reviewed.

X.1 SCULPTURE

In the *droogeri* lineage specimens may be smooth to highly sculptured. The degree of ornamentation is considered to be related to depth of habitat, ornate individuals having lived preferentially in deep parts of the depth range. Increased ornamentation is thought to be an adaptation to low light-intensity levels, as the sculptural elements may well have functioned as light-concentrating devices.

Ornamentation in the *droogeri* lineage shows a coarse aspect compared to the sculpture of the *koolhoveni* lineage and to the still more delicate features of *C. eidae*. The sculpture of the Ramla Cycloclypei may be considered as intermediate between those of the European *droogeri* assemblages and those of the Indonesian *koolhoveni* lineage. However, the data from these scattered occurrences are not sufficient to conclude to a continuous geographical cline in the type of ornamentation in these Oligocene Cycloclypei. In *C. eidae* no distinct differences in sculpture are apparent for its assemblages from the Mediterranean and Indo-Pacific regions.

We suggest that the species of the *droogeri* lineage grew at a relatively slow rate and spent more time between successive budding-steps than *C. koolhoveni* and *C. eidae*. A similar difference in growth activity was inferred by Jorissen (1988) for thickly calcified morphotypes with blunt and broad pustules and thinly calcified ones, which occur in the variation of Recent species of smaller benthic foraminifera.

Within the *droogeri* lineage no trend with time is apparent in the morphology of the sculpture.

X.2.1 Relations with depth

No data are available on depth related variation in the internal morphology of megalospheric specimens of *C. koolhoveni* and *C. eidae*. For the Cycloclypei of the *droogeri* lineage a relation could be reconstructed between depth of habitat and embryon-size but the differences were probably very small.

The clinal variation seems to be composed of two different elements. The data suggest that embryon-size slightly increased with increasing depth of habitat. This trend would have some relation with the concomitant decrease in light-intensity. Secondly, embryon-size may have been affected by depth related differences in population density. This effect may have been accomplished in two different ways, leading to similar results.

- In densely populated depth intervals, embryon-size may have become larger, at the expense of the number of offspring, to increase the viability of the juveniles.
- A similar increase in (mean) embryon-size may have been brought about if megalospheric individuals produced by microspheric parents had larger embryons than other megalospheres. If sexual reproduction was more successful in these densely populated areas, relatively more microspheric specimens were produced. This in turn may have resulted in an increase in the proportion of megalospheric specimens produced by microspheric parents.

Such density-induced effects may have occurred in the Ramla assemblages only, as only the Cycloclypei from this locality seem to have been present in large enough numbers to make significant density differences along a depth gradient feasible in the first place.

X.2.2 Biogeographical aspects

No distinct differences in embryon-size are apparent for the *eidae* assemblages from Europe and Indonesia. In the *koolhoveni* lineage embryon-size is larger than in the *droogeri* lineage. Again the Ramla Cycloclypei seem to be intermediate. If the relatively small embryon dimensions in the Mediterranean Cycloclypei are ascribed to the reduced light-incidence at higher latitudes, this effect would be opposite to the suggested increase in embryon-size in response to the reduced light-intensity levels at greater depth.

Therefore the small embryon dimensions in the *droogeri* lineage are alternatively considered to be an adaptation to the relatively low numbers in which these specimens occurred, as inferred from the enormous differences in the relative abundance of the genus in the Mediterranean and Indonesian samples.

X.2.3 Time-bound changes in embryon-size

X.2.3.1 The droogeri lineage

In the *droogeri* lineage an evolutionary increase is apparent in the size of the embryonic chambers. However, this increase is most distinct in the younger species of the lineage, *C. mediterraneus*, and less so in the ancestral *C. droogeri*. This course in evolutionary history is known in other groups of larger foraminifera as well. In the early part of phylogeny increase in embryon-size seems to be subordinate to the evolutionary reduction of the nepionic stage. Only in the later course of evolution embryon-size increase seems to grow more and more important, while nepionic development is waning.

A model was put forward by Drooger (1974) to explain this pattern. In this P-Q model it is assumed that it is of selective advantage for larger foraminifera to reduce size P at which cyclical (or radial) growth is reached. It would also be advantageous to attain large test-sizes in early ontogenetic stages up to some size Q, beyond which size increase would no longer be of advantage for the individual. In view of this latter assumption initial size would tend to increase but in the early phylogenetic stages this would seriously be counteracted by the implications of the former assumption, as according to Drooger the increase in embryon-size would result in a larger size P after p growth steps.

However, as shown by our study, in *Cycloclypeus* the size of the precyclic stage is not related to the size of the initial chambers. A larger embryon-size simply leads to a smaller number of growth steps p and not to a larger size P. Therefore the basic assumptions of the P-Q model do not fit the available data in the case of *Cycloclypeus* and we doubt whether the model may prove to be more successful in other cases.

Cycloclypeus and other larger foraminifera are best considered as K-strategists which strive to survive by making efficient use of limited resources. K-selected species are typically long-lived and large-sized and produce small numbers of juveniles. These characteristics result in large-sized young. Trends in embryon-size increase in larger foraminifera may thus be seen as a result of K-selection.

In this perspective end-members of lineages are more typically K-strategists than the more primitive ancestral forms. Perhaps the accelerated increase in embryon-size towards the end of phylogeny simply reflects a growing importance of K-selection. An alternative view on the relation of K-selection with embryonic and nepionic evolution will be developed in our final chapter.

X.2.3.2 The other lineages

Although relevant data are small in number, an overall increase in mean

embryon-size is apparent also in the Indonesian *koolhoveni* lineage. These Cycloclypei are succeeded by those of the *eidae* lineage with their significantly smaller embryons.

If it is accepted that the ancestral forms of *C. eidae* lived in a sparsely populated, marginal part of the distributional area of *C. koolhoveni*, we may expect that embryon-size in these Cycloclypei was already relatively small in view of our earlier considerations on the relation between population-density and the number of offspring in asexual reproduction. If we further accept that these Cycloclypei subsequently took over the largely or totally vacated area previously occupied by the main *koolhoveni* stock, densities may have dropped to still lower values. This may have stimulated a further increase in the numbers of young megalospheres produced in asexual reproduction, causing a further reduction in the initial volume of protoplasm. There is no evidence for such a gradual or step-wise reduction in embryon-size in early *C. eidae*. However, if our reconstruction of evolutionary events is a realistic one, this reduction in embryon-size is thought to have occurred in a relatively short time-span and we have to bear in mind that the record is far from perfect.

The suggested effect of population-density on embryon-size in early *C. eidae* was probably even reinforced by a larger carrying capacity of the former main distributional area of *C. koolhoveni*, as conditions are expected to have been more favourable than those prevailing in the marginal areas occupied previously. So in our concept there was not only a vast area to be colonized but also each unit of area could probably support a manyfold of the specimens supported by a similar area under marginal conditions. As this would have put a significant bonus on increased fertility, evolution, which proceeded towards a K-selected morphology, as reflected by the increase in embryon-size in the *koolhoveni* lineage, was possibly temporarily interrupted by a shift towards r-selection for increased fertility and embryon-size reduction.

From Tan's data it is not clear whether the *eidae*-types in the assemblages of *C. eidae* show an evolutionary increase in embryon-size. As these *eidae*-types become accompanied by increasing numbers of *carpenteri*-types with large embryons, mean embryon-size values based on total numbers of observations, tend to increase, if the assemblages are arranged in the stratigraphical order as assumed by Tan.

No evolutionary development in embryon-size could be recorded in the few data on our Mediterranean assembages of *C. eidae*. In this region, however, the genus became extinct at the end of the Oligocene or soon after the beginning of the Miocene.

X.3 NEPIONIC MORPHOLOGY IN SPACE AND TIME

In the megalospheric Cycloclypei of the *droogeri* lineage depth related changes have been observed in the precyclic stage. These differences were very small.

The changes in the number of precyclic chambers partly result from the concomitant changes in the size of the embryonic chambers discussed earlier. At Ramla large embryon-dimensions were considered to prevail in the middle part of the depth range. This larger initial volume of protoplasm reduced the number of growth steps necessary to reach the genetically 'fixed', ultimate size of the precyclic stage. In the Cycloclypei from this depth interval growth steps appeared to be larger than in specimens from shallower and deeper habitats, which in our concept further contributed to the reduction in the number of precyclic growth steps in this interval.

A third source of depth related variation in the number of precyclic chambers is constituted by variation in the size of the precyclic stage. In the European assemblages of the *droogeri* lineage the number of precyclic chambers seems to decrease with increasing depth as a result of a concomitant overall reduction in the size of the precyclic stage. This was not evident in the Ramla data set. However, it remains possible that at Ramla a similar depth related size reduction occurred. In that case it may have been too small to be detected by our biometrical methods or it may have occurred for instance at the deep end of the depth range only, which would only be poorly represented in our samples, if at all.

Geographical differences in the number of precyclic growth steps or in the size of the precyclic stage are difficult to detect. There is no independent biostratigraphical control by other groups of organisms showing an equally rapid evolutionary development. As mentioned previously, at Ramla the combination of these characters (X and D_X) appears to be different from all of the other, European assemblages of the *droogeri* lineage. The Ramla specimens show an extraordinarily small number of precyclic growth steps with respect to the size of the precyclic stage. This was thought to be related to the relatively larger size of the embryonic chambers at Ramla.

This suggests that there was some geographic difference in *C. mediterraneus* in the number of precyclic chambers that could have been related to the earlier discussed geographic difference in embryon-size.

In the *droogeri* lineage time-bound changes occurred in the precyclic stage. There is evidence for an almost continuous reduction in the number of nepionic chambers in response to a reduction in the size of the precyclic stage. Basically nepionic evolution in *Cycloclypeus* seems to consist of a change in the

relation between the size of the test at some nepionic stage i and the degree of embracing of the chamber formed during that stage. This means that at some size V the degree of embracing becomes larger during phylogeny and that the stage of total embracement (cyclical growth) is reached at a smaller size which in turn is reached in a smaller number of growth steps.

This means that the reduction in the number of nepionic chambers is a secondary effect and that the stage of nepionic evolution is more directly reflected by the size of the precyclic stage. However, it does not seem to be very practical to redefine the biometrical species of the genus *Cycloclypeus* on the basis of the size of the precyclic stage in stead of the number of precyclic chambers.

Although in the Mediterranean region the advanced members of the *droogeri* lineage were replaced by *C. eidae*, this immigrant species seems to be of relatively primitive build regarding the number of precyclic chambers. However, as its precyclic size is smaller than in advanced *C. mediterraneus*, it is still considered to be more highly developed in nepionic evolution.

A distinct difference is present in the number of precyclic chambers in *eidae*-types and *carpenteri*-types in our 'mixed' assemblage and in those of the Indo-Pacific. In our material the size of the precyclic stage is small in the few *carpenteri*-types, but not smaller than the smallest values reached by the *eidae*-types in the assemblage. Therefore the two types are not considered to differ greatly in their stage of nepionic evolution.

X.4 SIMILARITIES IN CLINES AND EVOLUTION

From our biometrical results the size of the precyclic stage appears to be rather independent of other morphometric features. It is not determined by embryon-size nor by rate of size increase. It is positively correlated with the number of precyclic chambers but this appeared to reflect a relation in which this number depended upon the size of the precyclic stage. It seems to be a genetically controlled character showing an evolutionary development.

Our data on the Spanish and Italian Cycloclypei therefore seem to suggest that deep-dwelling populations of the *droogeri* lineage, because of their smaller $\bar{D}_X$, were slightly more advanced in nepionic evolution than populations from shallower habitats. If this means that selection pressure was higher in these deep parts of the euphotic zone, a relation seems to be obvious with the low light-intensity levels prevailing here.

Light may be considered as a resource of vital importance for the combination of host and symbionts. Under these circumstances a more efficient use of this restricted resource or a growth strategy which was better adapted to the lower life activities of the symbionts and the host are expected to have been

highly advantageous. This may well be regarded as K-selection, which was already suggested to control the evolutionary processes in larger foraminifera in general. In this way low light-intensity levels may have stimulated nepionic evolution in the deep part of the euphotic zone. The increase in embryon-size with increasing depth in these European Cycloclypei may equally reflect such an increase in K-selection. This cline was already thought to be connected to decreasing light-intensities.

We have to acknowledge that at Ramla the situation was different. Embryon-size differences in depth populations were thought to be largely controlled by differences in population densities. A differentiation in size of the precyclic stage may have existed but could not be detected. This may have been the result of the size of the Ramla populations which were inferred to have been larger by far than those in the European region. Large population size has a buffering effect on changes in genetic composition.

Chapter XI

THE EVOLUTIONARY DEVELOPMENT OF OLIGOCENE CYCLOCLYPEUS

In this final chapter we will present our views on a number of topics which in our opinion are essential to the evolution of Oligocene *Cycloclypeus*.

XI.1 EMBRYON-SIZE AS A CONSERVATIVE CHARACTER

Our data on clinal variation in *Cycloclypeus* may have given the impression that embryon-size could change freely in response to local environmental conditions in order to attain an optimal combination of number of offspring in asexual reproduction and viability of the individual young. Secondly, the drastic reduction in embryon-size in the succession of *C. koolhoveni* by *C. eidae* seems to suggest that embryon dimensions have no relation with the stage of nepionic evolution as expressed by the number of precyclic growth steps. Furthermore it has become apparent that in *Cycloclypeus* the stage of nepionic evolution is more directly reflected by the size of the precyclic stage than by the number of precyclic growth steps. As there is no relation at the assemblage level between this precyclic test-size and the size of the embryonic chambers, the impression that embryon-size is independent of nepionic evolution is further enforced.

There are, however, decisive arguments to postulate that embryon-size in *Cycloclypeus* could not change that freely and is, in fact, a rather conservative character. The *droogeri* lineage shows a region-wide evolutionary increase in embryon-size, which is not expected to reflect an overall change in local conditions in the course of time or a change in preference for a deeper habitat. Clinal variation at any time was of very limited magnitude and probably only superimposed on a rather stable course of evolutionary increase in embryon-size. In the overall evolutionary history of the genus embryon-size increase is an on-going theme, that was seriously interrupted only once or twice.

XI.2 TEST MORPHOLOGY AND GROWTH CHARACTERISTICS

In *Cycloclypeus*, as in other multi-chambered foraminifera, test morphology is closely related to the pattern of individual growth, comprising the rate of protoplasm growth in time and the lapse of time between successive budding-steps. Chamber-volume is considered to be proportional to the increase in

protoplasm-volume at each budding-step. In turn, this increase is thought to be proportional to the total volume of protoplasm in the preceding stage. As shown by our morphometric study of the Ramla Cycloclypei this proportion tends to become reduced during ontogeny.

This means that the embryonic size is not only of importance for the chamber arrangement in the early ontogenetic stages. Specimens of large embryonic size are not identical in nepionic and neanic build to specimens with small embryons which reach a similar size only after a larger number of budding-steps. The proportions in the subsequent budding-steps will remain smaller than in the specimens which started life with a larger volume of protoplasm. Therefore the internal morphology of the test not only depends on the growth path followed during ontogeny but also on the size of the embryonic chambers.

Of course test morphology is also dependent on the shape and arrangement of the successive chambers. We may safely assume that the information which enables *Cycloclypeus* to build its test in its specific way and to restore damaged parts if necessary, is to a large extent hereditary in character. We suggest that the relative length of the chambers in the later part of the nepionic stage is part of this information and that this length depends on the size of the test reached at these budding-stages.

This building scheme would have to be coordinated with the pattern of protoplasm growth, followed during ontogeny. Otherwise, chambers formed for instance after little growth of protoplasm would be too small in height (plate 9 ,fig. 3). In this sense evolution in the nepionic morphology would simultaneously reflect

- an evolutionary development in the building scheme by an increase in the relative length of the chambers and
- a concomitant evolutionary increase in the volume of protoplasm grown during the lapse of time between successive budding-steps.

This suggests that the rate of protoplasm growth per time-unit increased during phylogeny. Such an increase in growth activity probably also would have increased the minimum environmental requirements of the host and its symbionts to support their life activities. By contrast, we expect that growth activity and life requirements become reduced in the process of K-selection. We therefore suggest that the evolutionary increase in chamber volume reflects an increase in the lapse of time between successive budding-steps rather than an increase in the rate of protoplasm growth per time-unit. Evolutionary change in the growth path of *Cycloclypeus* individuals could therefore be considered as an overall reduction in growth activity. This reduction would be expressed by

lower growth rates of the protoplasm and by longer periods of time between successive budding-steps. If furthermore growth activity already decreased during the life-time of our Cycloclypei, this would mean that in the course of evolution specimens started to grow more slowly earlier in life.

By no means do we wish to contest the selective advantage of the morphological result of an evolution in growth characteristics: The cyclical or radial organization of chambers is thought to fit the rather passive mode of life in symbiont bearing larger foraminifera very well. In our opinion this result in chamber arrangement contributed considerably to the success of advanced morphotypes of *Cycloclypeus*.

If the first appearance of *Cycloclypeus* was preceded by an evolutionary development in *Heterostegina*, a selective advantage of a cyclical chamber arrangement cannot be claimed in this case as in this genus all the chambers are arranged in a spiral. Therefore such an evolutionary development is thought to be based on a changing and more successful growth strategy, resulting in a development toward the *Cycloclypeus* morphology.

Two growth patterns were recognized in the Cycloclypei from Ramla. We suggest that the early pattern is typical of a *Heterostegina* morphology, while the later pattern leads to the morphology typical of *Cycloclypeus*. We furthermore suggest that the evolution in *Cycloclypeus* may basically consist of a shift of the second growth pattern toward earlier ontogenetic stages. It would therefore be interesting to check whether the break in the ontogenetic development, observed at Ramla at the stage of $i = 7$ on average, can be recognized in other localities as well. In that case we would expect it to show up in an ontogenetic later stage in more primitive assemblages and in an earlier stage in more advanced assemblages.

XI.3 THE INTERRELATION OF EMBRYONIC AND NEPIONIC EVOLUTION

In our opinion evolutionary increase in the initial volume of protoplasm may well be considered as an effort to compensate for a phylogenetic reduction in growth activity as outlined earlier. In the course of phylogeny increasing embryon dimensions would have to compensate the cumulative effect of lower rates of protoplasm growth per time-unit in successive stages. This may well have contributed to the growing importance of embryon-size increase during phylogeny. Moreover, in the course of phylogeny such reduced growth rates would have been introduced in earlier ontogenetic stages. The consequently slow increase in test-size in these early stages would mean that young specimens remained small -and more prone to predation- for an extended period of time.

Under these circumstances a larger initial size would be highly advantageous as it would reduce the time spent in the hazardous, small size-classes. Thus selection pressure for embryon-size increase would be higher than in the initial stages of nepionic evolution, resulting in the characteristic pattern in the evolutionary development of many groups of larger foraminifera.

In this way embryonic evolution in *Cycloclypeus* is thought to be intricately related to nepionic evolution. If the *koolhoveni-eidae* succession in Indonesia seems to suggest the opposite, we have to bear in mind that *C. eidae* shows a more delicate build in internal and external morphology than its predecessor and may therefore have had a distinctly different building plan and ontogenetic growth path than *C. koolhoveni*.

XI.4 THE LINK WITH CLINES

According to our reconstruction the depth related changes in the European Cycloclypei are similar in character to the time-bound changes in embryonic and nepionic evolution. Both the depth related changes in nepionic and in embryonic size were ascribed to more elevated levels of K-selection in the deeper and more stable part of the euphotic zone in response to low light intensities. It now appears that these depth related changes may be interrelated in a similar way as the phylogenetic changes, reduced growth activity in the deep-dwelling populations being compensated by an increase in the initial volume of protoplasm.

However, light-intensity seems to have been a limiting ecological factor for *Cycloclypeus* only in the deep part of its depth range, as for instance optimum conditions were considered to have prevailed in the middle part. This was largely inferred from the Ramla data but it is not thought to have been essentially different for European *Cycloclypeus*. Therefore, advanced morphotypes may have preferentially originated in the deep zones, increased in numbers there and were subsequently passed through to shallower zones. The sluggishness of the spreading process may have entailed a morphological gradient as suggested by our data.

Also, we have to bear in mind that in the shallow parts of the depth range little selective advantage may have remained for the advanced morphology. In this part of the photic zone spirally arranged Nummulitids were most probably more abundant and therefore more successful than a more typical K-strategist like *Cycloclypeus*.

We therefore maintain that the cline in European *Cycloclypeus* reflects a gradient favouring relative r-strategists in shallow waters and relative K-strategists in the deeper parts of the depth range. This may have been related to en-

vironmental instability due to seasonality in shallow waters. K-selection would have prevailed in the more stable environments in the deeper part of the depth range of *Cycloclypeus*, where the effects of seasonality would have been less pronounced.

Our line of reasoning seems to suggest that at least in the Mediterranean *droogeri* lineage evolution was to some extent propelled by deep-dwelling populations. This would provide a link between space-related and time-bound changes in the morphology of these Cycloclypei.

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PLATE 1

Cycloclypeus mediterraneus from Ramla, Israel.
All magnifications: × 12.5.
Fig. 1. 'Inornate' specimen of morphogroup A.
Figs. 2, 3. 'Intermediate' specimens of morphogroup B.
Fig. 4. 'Ornate' specimen of morphogroup C showing ridges overlying the septa.
Fig. 5. 'Ornate' specimen of morphogroup C showing sharply bound, thin pustules.

Plate 1

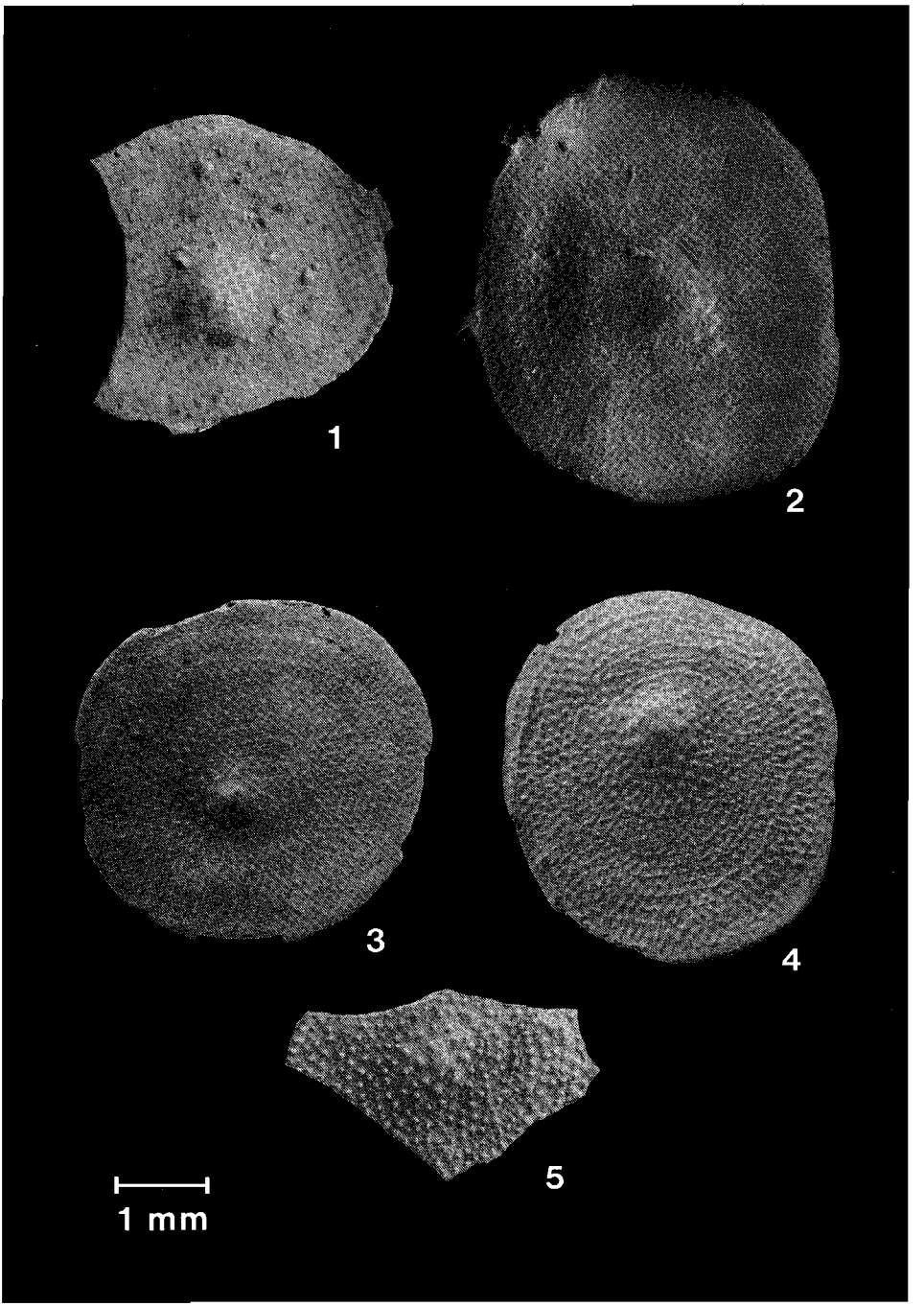


PLATE 2

Cycloclypeus mediterraneus from Ramla, Israel.

Fig. 1. Detail of 'intermediate' specimen figured on plate 1, fig. 3, showing zonation in ornamentation (magn. × 25).

Fig. 2. 'Ornate' specimen of morphogroup C with occasional septa overlain by two pustules (magn. × 12.5).

Plate 2

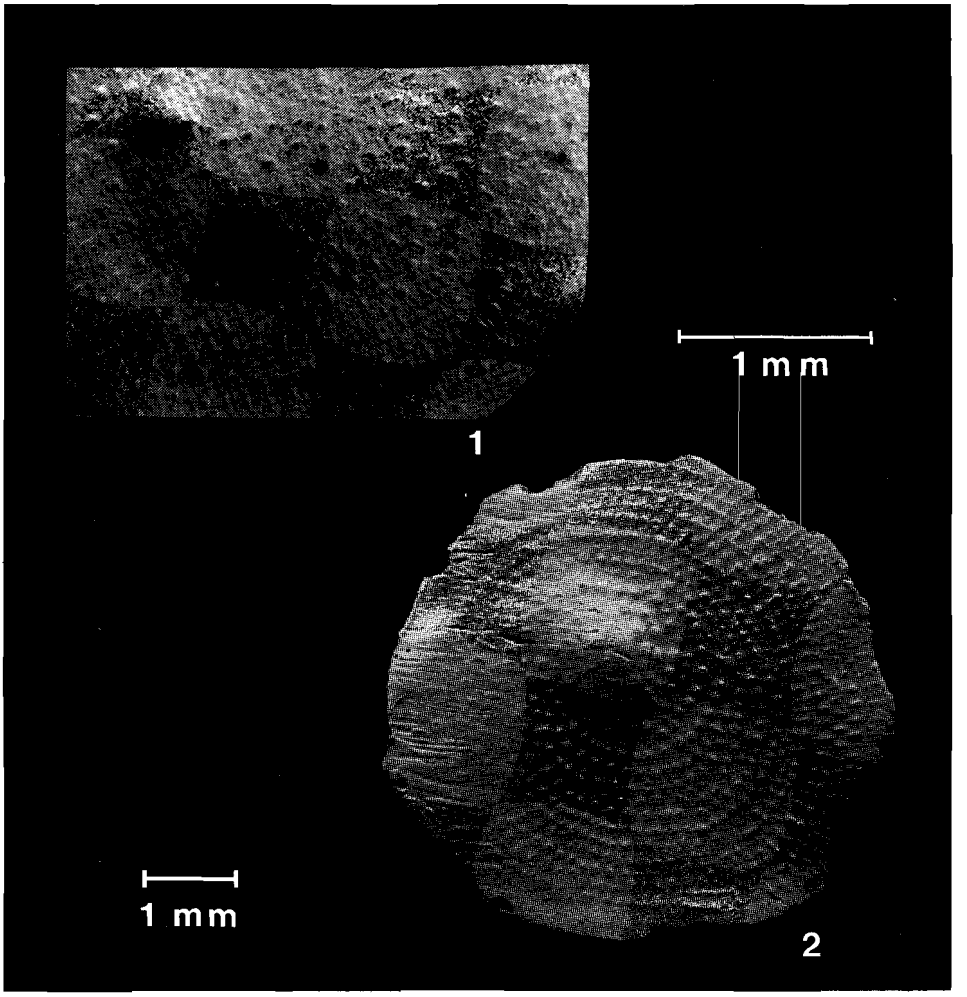


PLATE 3

Figs. 1 - 3. *Cycloclypeus eidae* from sample SP935, Granada, Spain (magn. × 12.5). Note the delicate and uniform ornamentation relative to the ornamentation of the Cycloclypei of the *droogeri*-lineage on plates 1 and 2.

Plate 3

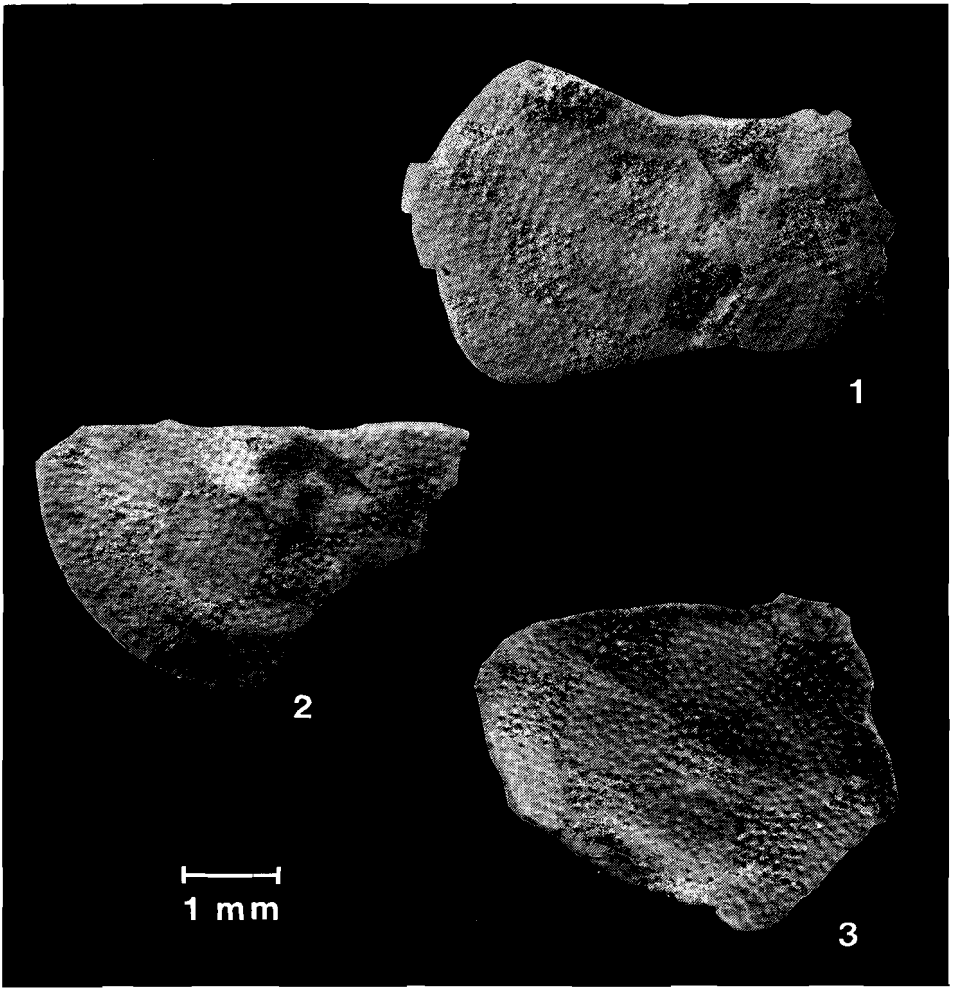


PLATE 4

Figs. 1, 2. *Cycloclypeus koolhoveni* from Tjimanggoe, Java, Indonesia (magn. × 12.5). Note the delicate, numerous and closely set pustules.

Plate 4

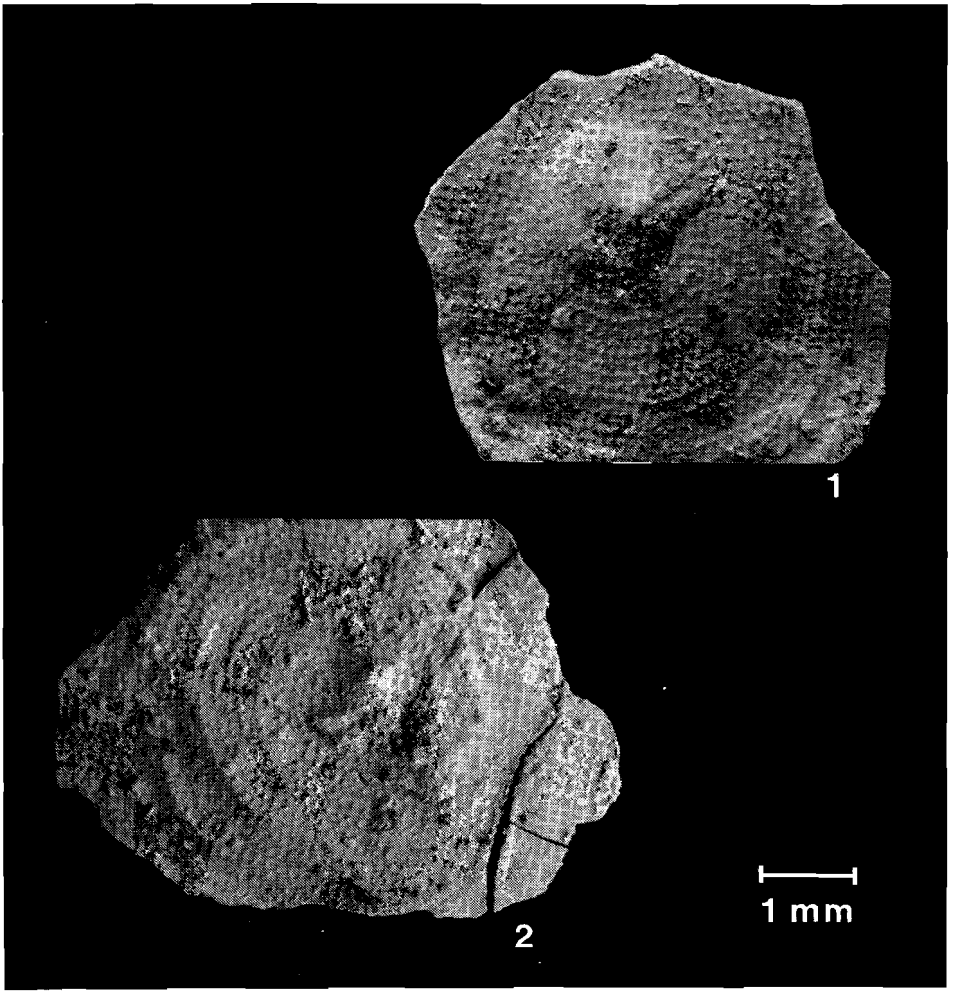


PLATE 5

Cycloclypeus carpenteri, Recent.

Fig. 1. Fragment (magn. × 12.5).

Fig. 2. Detail, showing imperforate ornaments with adjacent openings of canal-system (magn. × 250).

Fig. 3. Detail of cross-section, showing perforated side-wall and imperforate prisma-shaped section through pustule. On the right side of this pustule an adjacent opening of the canal-system is cut (magn. × 250).

Plate 5

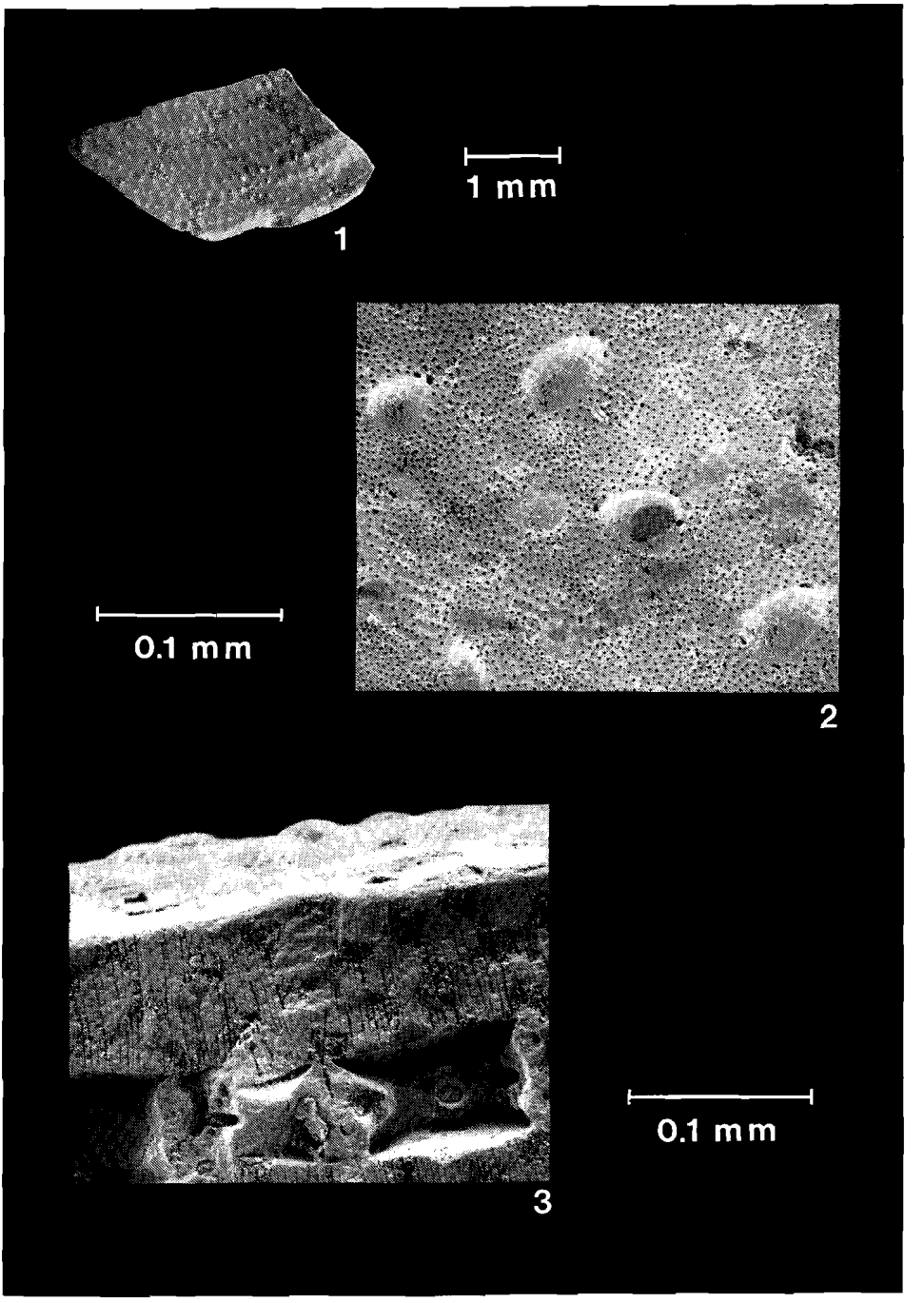


PLATE 6

Figs. 1, 2. *Cycloclypeus koolhoveni.* Camera lucida drawings of sectioned specimens from Tjimanggoe, Java, Indonesia (magn. × 20). Note the rapid increase in height of whorls and the large size of the precyclic stage relative to the specimens of other lineages on plates 7 to 9.

Plate 6

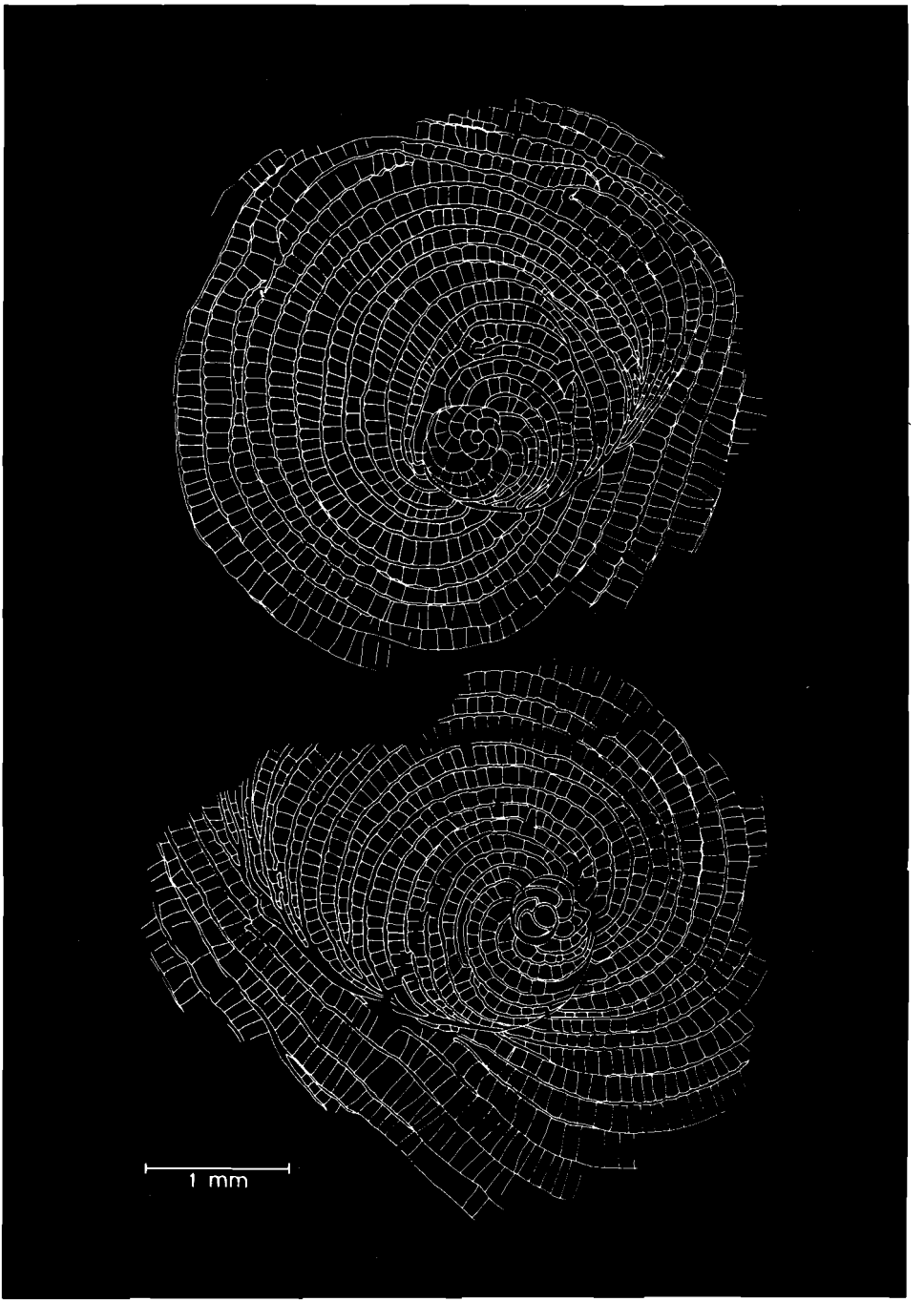


PLATE 7

Figs. 1, 2. *Cycloclypeus droogeri*. Camera lucida drawings of sectioned specimens from Lanuza, Alicante, Spain (magn. × 20).

Plate 7

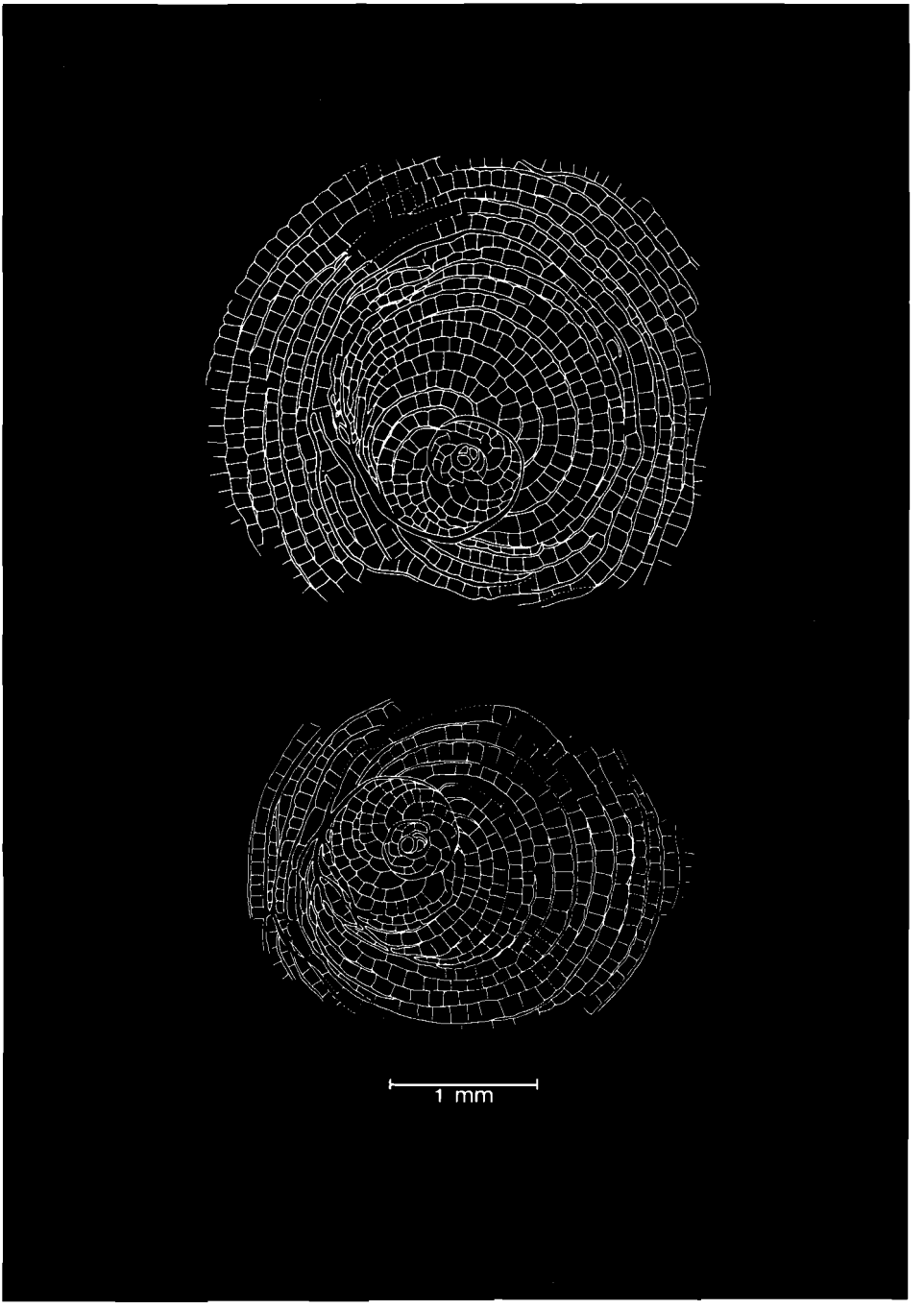


PLATE 8

Figs. 1, 2. *Cycloclypeus mediterraneus.* Camera lucida drawings of sectioned specimens from Ramla, Israel (magn. × 20).

Plate 8

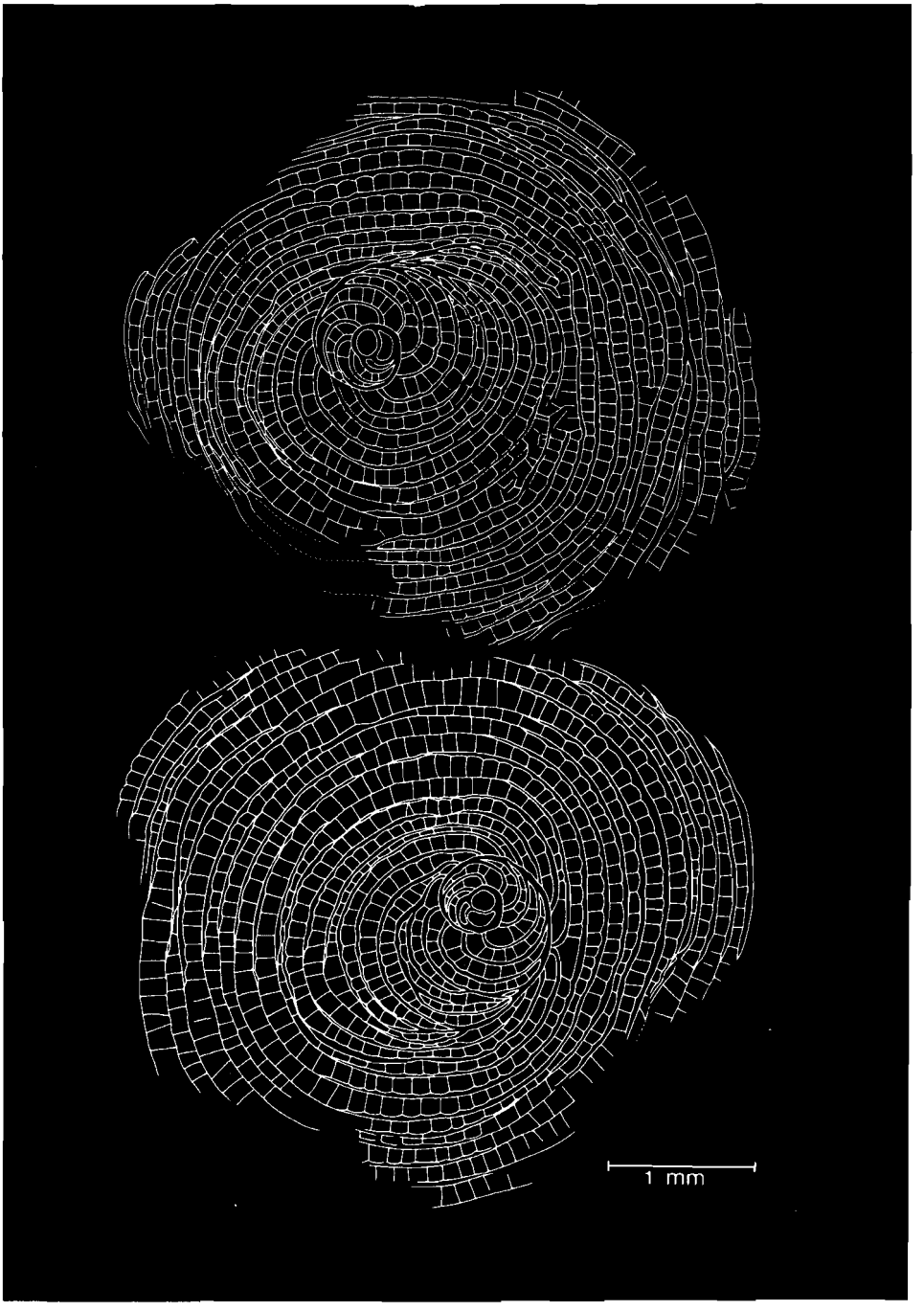


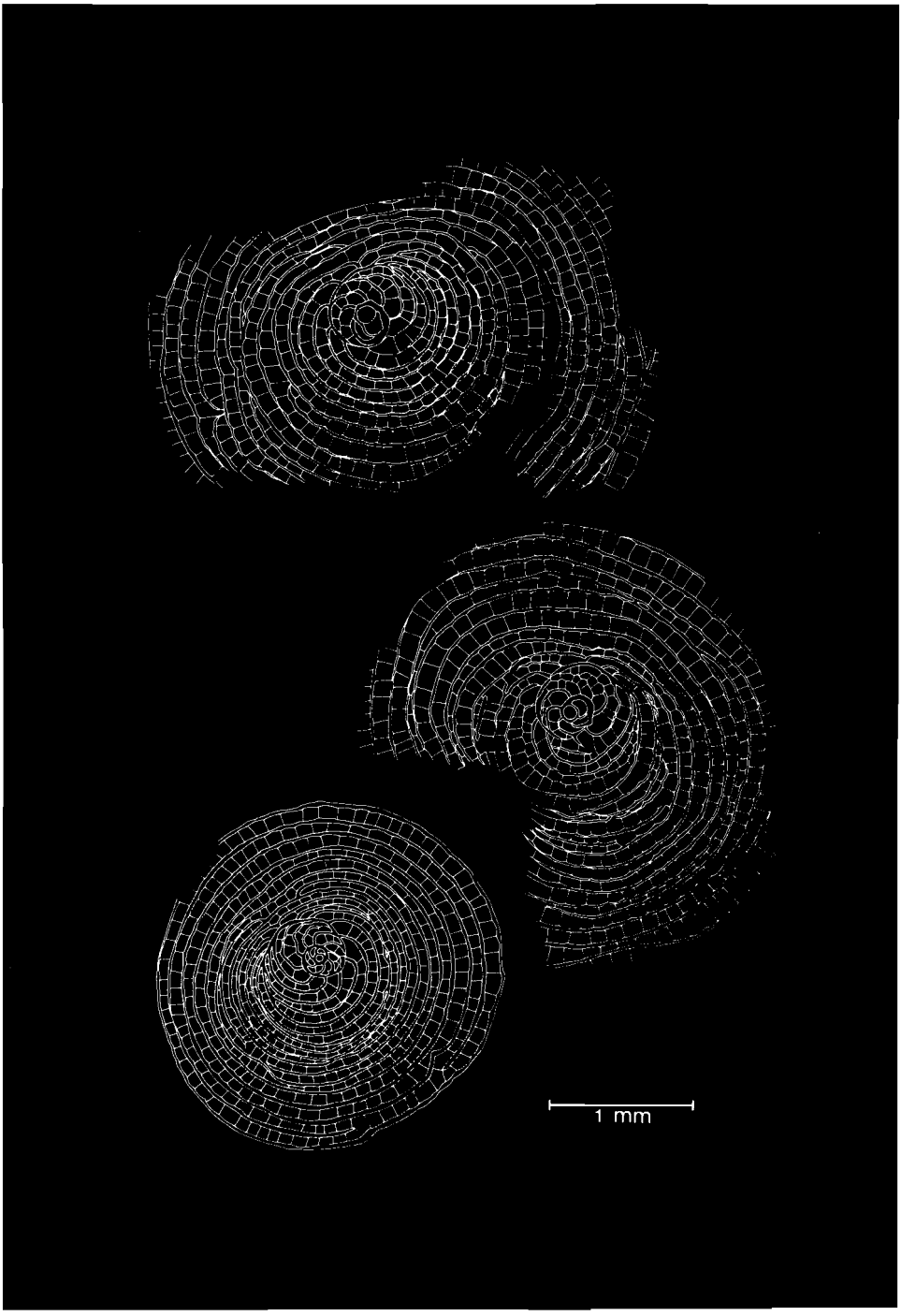
PLATE 9

Fig. 1. *Cycloclypeus mediterraneus*. Camera lucida drawing of sectioned specimen from L'Aquila, Italy (magn. × 20).

Fig. 2. *Cycloclypeus mediterraneus*. Camera lucida drawing of sectioned specimen from Lanuza, Alicante, Spain (magn. × 20).

Fig. 3. *Cycloclypeus eidae*. Camera lucida drawing of sectioned specimen from Malta. Material Drooger and Roelofsen (1982), collection State University Utrecht (magn. × 20). Note the small embryon and the delicate meshwork of chamber- and chamberlet-walls relative to the specimens of other lineages.

Plate 9



	I (μ)					II (μ)					X					γ (°)			
sample	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE
SP707	9	98	12	4	12.0	8	95	20	7	20.7	9	28.0	3.2	1.1	11.3	9	-494	60	20
SP842	7	101	9	3	8.8	7	82	15	6	17.9	5	24.8	1.3	0.6	5.3	5	-452	11	5
JT7911	6	98	6	3	6.2	5	97	10	5	10.7	5	22.6	3.2	1.4	14.2	9	-430	48	16
SP935	24	179	63	13	35.1	24	188	70	14	37.4	24	10.6	2.8	0.6	26.0	24	-110	86	18
SP936	50	126	35	5	28.0	43	130	41	6	31.5	51	15.7	2.7	0.4	17.4	51	-241	65	9
SP937	22	187	63	13	33.4	21	183	65	14	35.3	22	12.4	2.4	0.5	19.4	22	-138	73	16
SP938	37	131	29	5	21.8	36	134	29	5	21.7	35	13.6	2.7	0.5	19.8	37	-197	66	11
SP943	15	180	58	15	32.4	15	187	60	16	32.3	15	12.5	3.6	0.9	28.7	15	-150	88	23

TABLE I: Mean parameter values and associated statistics for the *Miogypsina* assemblages.

	d_1 (μ)					c_{12} (μ)					X					γ (°)				
sample	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V
SP808	55	122	20	3	16.5	56	174	28	4	16.3	33	30.1	4.0	0.7	13.2	38	876	69	11	7.9
SP810	72	121	21	2	17.0	72	179	30	4	16.7	50	25.9	3.9	0.6	15.2	53	793	82	11	10.4
SP816	28	128	23	4	17.9	28	194	49	9	25.2	19	25.8	3.0	0.7	11.7	23	784	83	17	10.5
SP818	58	121	25	3	21.0	58	182	34	5	18.9	40	24.2	3.2	0.5	13.3	47	770	82	12	10.6
SP820	30	134	20	4	14.7	30	196	28	5	14.4	28	20.9	2.6	0.5	12.3	28	707	69	13	9.7
SP825	76	130	27	3	20.8	76	190	39	4	20.3	58	20.9	3.2	0.4	15.5	60	698	96	12	13.7
SP827	31	128	22	4	17.5	31	186	33	6	18.0	21	22.0	3.8	0.8	17.2	21	730	93	20	12.7
SP831	74	145	29	3	19.7	73	211	38	4	18.0	43	20.1	3.7	0.6	18.2	49	664	96	14	14.5
SP835	67	155	27	3	17.3	67	225	41	5	18.4	51	18.3	3.1	0.4	16.9	58	627	85	11	11.1
SP836	52	153	38	5	24.9	52	222	52	7	23.6	38	19.5	4.7	0.8	24.1	44	668	130	20	19.4
SP839	40	152	37	6	24.3	40	222	50	8	22.6	32	19.0	4.6	0.8	24.3	35	644	112	19	17.3
SP841	31	164	28	5	17.0	32	237	45	8	19.0	30	17.1	3.5	0.6	20.5	30	582	88	16	15.1
SP842	89	164	29	3	17.7	89	232	38	4	16.3	58	16.5	3.1	0.4	19.0	61	582	89	11	15.3

TABLE II: Mean parameter values and associated statistics in the samples from Lanuza, Alicante.

	$d_1 - c_{12}$			$d_1 - X$			$d_1 - \gamma$			$X - \gamma$		
sample	N	r	S	N	r	S	N	r	S	N	r	S
SP808	55	0.91	+	31	-0.18		36	-0.57	+	33	0.75	+
SP810	72	0.94	+	50	-0.45	+	53	-0.62	+	50	0.82	+
SP816	28	0.88	+	19	-0.46	o	23	-0.65	+	19	0.78	+
SP818	58	0.89	+	40	-0.38	o	47	-0.64	+	40	0.87	+
SP820	30	0.95	+	28	-0,48	+	28	-0.68	+	28	0.80	+
SP825	76	0.91	+	58	-0.48	+	60	-0.70	+	58	0.89	+
SP827	31	0.89	+	21	-0.58	+	21	-0.78	+	21	0.85	+
SP831	73	0.92	+	43	-0.61	+	49	-0.72	+	43	0.93	+
SP835	67	0.89	+	51	-0.42	+	58	-0.57	+	51	0.86	+
SP836	52	0.95	+	37	-0.68	+	42	-0.78	+	38	0.96	+
SP839	40	0.96	+	31	-0.70	+	34	-0.80	+	32	0.94	+
SP841	31	0.85	+	29	-0.60	+	29	-0.68	+	30	0.94	+
SP842	89	0.89	+	58	-0.53	+	61	-0.67	+	58	0.90	+

TABLE III: Correlation coefficients of selected parameter combinations in the samples from Lanuza, Alicante. Significance levels o: $p < 0.05$
+: $p < 0.01$

	d_1 (μ)					c_{12} (μ)					X					γ (°)				
sample	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V
SP724	38	117	24	4	20.3	38	166	26	4	15.6	28	31.3	3.7	0.7	11.9	31	891	87	16	9.8
SP729	214	123	21	1	17.5	214	178	29	2	16.1	158	28.6	3.3	0.3	11.5	164	854	77	6	9.0
SP707	202	154	29	2	18.8	202	223	38	3	16.9	184	17.6	3.0	0.2	17.0	192	615	86	6	14.0
JT7911	113	149	29	3	19.4	113	216	41	4	19.0	92	16.1	2.5	0.3	15.5	101	586	77	8	13.1
IR469 IR470	264	164	27	2	16.7	261	240	38	2	16.0	231	20.2	2.7	0.2	13.5	241	667	74	5	11.1

TABLE IV: Mean parameter values and associated statistics in scattered Mediterranean samples.

	$d_1 - c_{12}$			$d_1 - X$			$d_1 - \gamma$			$X - \gamma$		
sample	N	r	S	N	r	S	N	r	S	N	r	S
SP724	38	0.82	+	28	-0.58	+	31	-0.72	+	28	0.90	+
SP729	214	0.91	+	158	-0.41	+	164	-0.71	+	158	0.76	+
SP707	202	0.92	+	183	-0.63	+	191	-0.79	+	182	0.87	+
JT7911	113	0.96	+	92	-0.61	+	101	-0.73	+	91	0.90	+
IR469 IR470	261	0.90	+	231	-0.54	+	241	-0.70	+	231	0.83	+

TABLE V: Correlation coefficients of selected parameter combinations in scattered Mediterranean samples. Significance levels o: $p < 0.05$
+: $p < 0.01$

	d_1 (μ)					c_{12} (μ)					X					γ (°)				
sample	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V
SP933	32	127	22	4	17.0	32	180	29	5	16.2	29	26.9	2.9	0.5	10.7	31	835	64	11	7.6
SP934	5	145	12	5	8.4	5	196	13	6	6.8	5	20.2	0.8	0.4	4.1	4	683	33	17	4.8
SP935	77	89	24	3	26.8	77	146	34	4	22.9	72	17.2	2.7	0.3	15.4	76	660	90	10	13.6
SP936	40	90	21	3	24.0	40	145	32	5	21.7	35	18.2	2.8	0.5	15.2	37	672	80	13	11.9
SP937	15	85	21	5	24.5	15	143	30	8	21.0	14	18.4	2.5	0.7	13.4	14	672	84	22	12.5
SP939	30	124	18	3	14.3	30	181	26	5	14.5	28	24.4	3.2	0.6	13.2	29	762	63	12	8.3
SP938	30	77	19	4	25.1	30	127	30	6	23.8	28	19.1	2.3	0.4	12.2	30	725	87	16	12.0
SP943	26	83	22	4	26.3	26	137	27	5	19.6	23	18.0	2.6	0.5	14.2	25	692	71	14	10.3

TABLE VI: Mean parameter values and associated statistics in the samples from the Navazuelo section and other localities in the Granada province.

	d_1 - c_{12}			d_1 - X			d_1 - γ			X - γ		
sample	N	r	S	N	r	S	N	r	S	N	r	S
SP933	31	0.93	+	28	-0.36	o	30	-0.79	+	28	0.67	+
SP934	5	0.72		5	0.00		4	0.71		4	-0.45	
SP935	77	0.95	+	72	-0.72	+	76	-0.86	+	72	0.86	+
SP936	40	0.95	+	35	-0.20		37	-0.61	+	34	0.83	+
SP937	15	0.95	+	14	-0.77	+	14	-0.74	+	14	0.87	+
SP939	30	0.84	+	28	-0.65	+	29	-0.78	+	28	0.87	+
SP938	30	0.90	+	28	-0.62	+	30	-0.73	+	28	0.89	+
SP943	26	0.91	+	22	-0.65	+	24	-0.52	+	23	0.87	+

TABLE VII: Correlation coefficients of selected parameter combinations in the samples from the Navazuelo section and other localities in the Granada province. Significance levels
o: $p < 0.05$
+: $p < 0.01$

X	N_x	F_x (%)	X	N_x	F_x (%)	X	N_x	F_x (%)
9	1	0.1	20	110	7.7	31	35	2.5
10	3	0.2	21	83	5.8	32	23	1.6
11	5	0.4	22	81	5.7	33	8	0.6
12	9	0.6	23	70	4.9	34	11	0.8
13	33	2.3	24	60	4.2	35	6	0.4
14	42	2.9	25	47	3.3	36	3	0.2
15	74	5.2	26	55	3.9	37	2	0.1
16	121	8.5	27	45	3.2	38	2	0.1
17	126	8.8	28	35	2.5	39	1	0.1
18	135	9.5	29	40	2.8	40	0	0.0
19	124	8.7	30	36	2.5	41	2	0.1

TABLE VIII: Absolute and relative frequencies of X-variants in all Mediterranean samples together except for SP710.

			D_X (mm)				
sample	N	(N_{tot})	M	SD	SE	V	species
SP729	36	(105)	2.52	0.42	0.07	16.6	*droogeri*
SP818	17	(58)	1.94	0.40	0.10	20.7	*droogeri*
SP825	21	(76)	1.68	0.49	0.11	29.0	*mediterraneus*
SP842	39	(89)	1.40	0.26	0.04	18.5	*mediterraneus*
SP707	158	(202)	1.44	0.25	0.02	17.5	*mediterraneus*
SP935	60	(77)	1.08	0.17	0.02	15.5	*eidae*
JT7911	86	(113)	1.28	0.26	0.03	20.2	*mediterraneus*
IR469 IR470	148	(264)	2.02	0.28	0.02	14.0	*mediterraneus*

TABLE IX: Mean values and associated statistics of parameter D_X in various Mediterranean samples. Megalospheric specimens only.

	d_1 - D_X			c_{12} - D_X			X - D_X			γ - D_X			
sample	N	r	S	N	r	S	N	r	S	N	r	S	species
SP729	36	0.26		36	0.27		34	-0.31		34	-0.37	o	*droogeri*
SP818	17	0.41		17	0.25		17	0.53	o	17	0.35		*droogeri*
SP825	21	0.26		21	0.37		21	0.64	+	21	0.45	o	*mediterraneus*
SP842	39	-0.01		39	-0.04		39	0.57	+	39	0.42	+	*mediterraneus*
SP707	157	-0.07		157	-0.05		153	0.61	+	157	0.39	+	*mediterraneus*
SP935	60	-0.28	o	60	-0.22		58	0.54	+	60	0.35	+	*eidae*
JT7911	86	0.19		86	0.17		82	0.45	+	83	0.25	o	*mediterraneus*
IR469 IR470	148	-0.04		146	-0.09		144	0.57	+	147	0.35	+	*mediterraneus*

TABLE X: Correlation coefficients of parameter combinations involving D_X in various Mediterranean samples. Megalospheric specimens only.
Significance levels o: $p < 0.05$
+: $p < 0.01$

SP729

	d_1 (μ)					c_{12} (μ)					X					γ (°)				
	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V
A	61	122	20	3	16.6	61	176	29	4	16.2	50	29.1	3.1	0.4	10.8	52	865	76	11	8.8
B	93	124	21	2	16.7	93	180	28	3	15.8	71	28.0	3.3	0.4	11.9	72	841	74	9	8.8
C	23	128	28	6	21.7	23	183	36	7	19.5	12	27.1	3.4	1.0	12.6	13	828	105	29	12.7

SP707

	d_1 (μ)					c_{12} (μ)					X					τ (°)				
	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V
A	62	157	30	4	18.9	62	226	41	5	18.0	57	18.0	3.1	0.4	17.3	58	621	87	11	14.1
B	118	153	26	2	17.1	118	222	34	3	15.3	109	17.5	2.9	0.3	16.8	113	612	81	8	13.2
C	22	155	41	9	26.4	22	226	49	11	21.8	18	17.6	3.1	0.7	17.5	21	615	109	24	17.8

JT7911

	d_1 (μ)					c_{12} (μ)					X					γ (°)				
	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V
A	12	149	25	7	16.8	12	217	40	12	18.5	10	16.6	3.0	0.9	17.8	9	594	81	27	13.6
B	27	152	27	5	17.6	27	221	37	7	16.6	21	16.1	2.4	0.5	14.6	24	585	75	15	12.8
C	34	158	33	6	20.9	34	225	48	8	21.1	30	15.7	2.7	0.5	16.9	31	573	84	15	14.7

TABLE XI: Mean parameter values and associated statistics of the three morphogroups in SP729, SP707 and JT7911.

SP729

	d_1 (μ)				c_{12} (μ)				X				γ (°)			
	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE
A	61	-0.09	0.94	0.12	61	-0.11	0.97	0.12	50	0.22	0.95	0.13	52	0.21	0.96	0.13
B	93	0.01	0.96	0.10	93	0.04	0.96	0.10	71	-0.09	1.01	0.12	72	-0.10	0.94	0.11
C	23	0.19	1.29	0.27	23	0.13	1.21	0.25	12	-0.38	1.04	0.30	13	-0.27	1.34	0.37

SP707

	d_1 (μ)				c_{12} (μ)				X				γ (°)			
	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE
A	62	0.09	1.02	0.13	62	0.06	1.07	0.14	57	0.12	1.04	0.14	58	0.07	1.02	0.13
B	118	-0.06	0.90	0.08	118	-0.04	0.90	0.08	109	-0.06	0.98	0.09	113	-0.03	0.94	0.09
C	22	0.03	1.41	0.30	22	0.06	1.31	0.28	18	-0.02	1.03	0.24	21	0.00	1.27	0.28

LANUZA-1

	d_1 (μ)				c_{12} (μ)				X				γ (°)			
	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE
A	29	-0.08	1.12	0.21	29	-0.11	1.01	0.19	22	0.19	1.19	0.25	25	0.12	1.13	0.23
B	50	0.04	0.96	0.14	50	0.06	1.01	0.14	36	-0.12	0.84	0.14	40	-0.10	0.90	0.14
C	10	0.01	0.69	0.22	10	0.03	0.85	0.27	7	0.02	0.92	0.35	8	0.13	0.93	0.33

LANUZA-2

	d_1 (μ)				c_{12} (μ)				X				γ (°)			
	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE
A	16	-0.24	0.95	0.24	16	-0.19	0.88	0.22	16	0.17	1.07	0.27	16	0.26	1.01	0.25
B	123	-0.02	0.96	0.09	124	0.00	0.98	0.09	109	0.10	0.97	0.09	114	0.06	0.96	0.09
C	30	0.19	1.07	0.19	30	0.10	1.01	0.19	27	-0.52	0.77	0.15	30	-0.38	0.92	0.17

JT7911

	d_1 (μ)				c_{12} (μ)				X				γ (°)			
	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE
A	12	-0.17	0.85	0.25	12	-0.13	0.95	0.27	10	0.23	1.14	0.36	9	0.18	1.02	0.34
B	27	-0.07	0.91	0.18	27	-0.04	0.87	0.17	21	0.05	0.91	0.20	24	0.05	0.94	0.19
C	34	0.12	1.12	0.19	34	0.08	1.13	0.19	30	-0.11	1.03	0.19	31	-0.09	1.06	0.19

ALL DATA

	d_1 (μ)				c_{12} (μ)				X				γ (°)			
	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE
A	180	-0.04	0.99	0.07	180	-0.06	0.99	0.07	155	0.18	1.03	0.08	160	0.15	1.01	0.08
B	411	-0.02	0.93	0.05	412	0.00	0.95	0.05	346	-0.01	0.96	0.05	363	-0.02	0.94	0.05
C	119	0.13	1.16	0.11	119	0.09	1.11	0.10	94	-0.24	0.96	0.10	103	-0.16	1.09	0.11

TABLE XII: Standardized mean parameter values and associated statistics of the three morphogroups in five European (lump-)samples.

TABLE XIII: Standardized mean parameter values and associated statistics of the three morphogroups calculated from the total number of European data.

d_1 - X

	A			B			C			A + B + C		
sample	N	r	S	N	r	S	N	r	S	N	r	S
SP729	50	-0.54	+	71	-0.30	+	12	-0.65	o	133	-0.43	+
SP707	57	-0.56	+	108	-0.67	+	18	-0.76	+	183	-0.63	+
LANUZA-1	22	-0.47	o	36	-0.28		7	-0.66		65	-0.39	+
LANUZA-2	16	-0.54	o	107	-0.61	+	27	-0.22		150	-0.55	+
JT7911	10	-0.30		21	-0.60	+	30	-0.63	+	61	-0.57	+
ALL DATA	155	-0.52	+	343	-0.53	+	94	-0.59	+	592	-0.54	+

d_1 - γ

	A			B			C			A + B + C		
sample	N	r	S	N	r	S	N	r	S	N	r	S
SP729	52	-0.79	+	72	-0.64	+	13	-0.88	+	137	-0.73	+
SP707	58	-0.75	+	112	-0.79	+	21	-0.90	+	191	-0.79	+
LANUZA-1	25	-0.66	+	40	-0.63	+	8	-0.73	o	73	-0.65	+
LANUZA-2	16	-0.64	+	111	-0.71	+	30	-0.59	+	157	-0.68	+
JT7911	9	-0.68	o	24	-0.61	+	31	-0.76	+	64	-0.71	+
ALL DATA	160	-0.73	+	359	-0.70	+	103	-0.78	+	622	-0.73	+

TABLE XIV: Correlation coefficients of parameter pairs d_1-X and d_1-γ calculated for the three morphogroups separately and for all specimens together in five European (lump-)samples as well as in all these samples together.
Significance levels o: $p < 0.05$
+: $p < 0.01$

d_1 - X

	A			B			C			A + B + C		
sample	N	r	S	N	r	S	N	r	S	N	r	S
IR469	34	-0.64	+	74	-0.49	+	40	-0.61	+	148	-0.57	+
IR470	3	-		53	-0.61	+	27	-0.40	o	83	-0.50	+
ALL DATA	37	-0.57	+	127	-0.54	+	67	-0.51	+	231	-0.54	+

d_1 - γ

	A			B			C			A + B + C		
sample	N	r	S	N	r	S	N	r	S	N	r	S
IR469	36	-0.84	+	77	-0.64	+	42	-0.71	+	155	-0.72	+
IR470	3	-		56	-0.70	+	27	-0.57	+	86	-0.65	+
ALL DATA	39	-0.82	+	133	-0.66	+	69	-0.64	+	241	-0.70	+

TABLE XVII: Correlation coefficients of parameter pairs d_1-X and d_1-γ calculated for the three morphogroups separately and for all specimens together in samples IR469 and IR470 and in both samples together. Significance levels o: $p < 0.05$
+: $p < 0.01$

IR469

	d_1 (μ)					c_{12} (μ)					X					γ (°)				
	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V
A	39	159	29	5	18.1	39	235	41	7	17.3	34	20.8	3.1	0.5	14.8	36	675	86	14	12.7
B	85	169	25	3	14.9	83	251	35	4	13.7	74	19.7	2.8	0.3	14.2	77	649	69	8	10.7
C	46	163	26	4	16.2	46	235	33	5	14.3	40	20.3	2.4	0.4	11,9	42	676	65	10	9.6

IR470

	d_1 (μ)					c_{12} (μ)					X					γ (°)				
	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V
A	3	150	-	-	-	3	235	-	-	-	3	23.3	-	-	-	3	700		-	-
B	61	166	27	3	16.2	'61	243	39	5	16.0	53	20.0	2.5	0.3	12.4	56	665	68	9	10.2
C	30	151	30	6	20.0	29	215	42	8	19.7	27	20.4	2.7	0.5	13.1	27	693	89	17	12.8

ALL DATA

	d_1 (μ)					c_{12} (μ)					X					γ (°)				
	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V	N	M	SD	SE	V
A	42	158	28	4	17.7	42	235	39	6	16.7	37	21.0	3.2	0.5	15.1	39	677	83	13	12.3
B	146	168	26	2	15.4	144	248	37	3	14.7	127	19.9	2.7	0.2	13.4	133	656	69	6	10.5
C	76	158	28	3	18.0	75	227	38	4	16.8	67	20.4	2.5	0.3	12.3	69	683	75	9	11.0

TABLE XV: Mean parameter values and associated statistics of the three morphogroups in IR469 and IR470 as well as in both samples together.

IR469

	d_1 (μ)				c_{12} (μ)				X				γ (°)			
	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE
A	39	-0.24	1.08	0.17	39	-0.22	1.11	0.18	34	0.24	1.11	0.19	36	0.17	1.17	0.20
B	85	0.16	0.95	0.10	83	0.23	0.95	0.10	74	-0.15	1.00	0.12	77	-0.18	0.95	0.11
C	46	-0.09	0.99	0.15	46	-0.23	0.92	0.13	40	0.06	0.87	0.14	42	0.18	0.89	0.14

IR470

	d_1 (μ)				c_{12} (μ)				X				γ (°)			
	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE
A	3	-0.37	-	-	3	0.02	-	-	3	1.16	-	-	3	0.33	-	-
B	61	0.19	0.94	0.12	61	0.22	0.94	0.12	53	-0.10	0.94	0.13	56	-0.13	0.91	0.12
C	30	-0.35	1.06	0.19	29	-0.46	1.03	0.19	27	0.06	1.01	0.20	27	0.24	1.18	0.23

ALL DATA

	d_1 (μ)				c_{12} (μ)				X				γ (°)			
	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE	N	M	SD	SE
A	42	-0.20	1.02	0.16	42	-0.13	1.02	0.16	37	0.31	1.16	0.19	39	0.14	1.12	0.18
B	146	0.16	0.95	0.08	144	0.21	0.95	0.08	127	-0.13	0.98	0.09	133	-0.15	0.93	0.08
C	76	-0.20	1.04	0.12	75	-0.33	0.99	0.11	67	0.07	0.92	0.11	69	0.21	1.01	0.12

TABLE XVI: Standardized version of Table XV.

SP729

	D_x (mm)					D_x (stand.)			
	N	M	SD	SE	V	N	M	SD	SE
A	14	2.47	0.22	0.6	8.7	14	-0.10	0.52	0.14
B	19	2.50	0.47	0.11	18.7	19	-0.03	1.12	0.26
C	3	2.80	0.80	0.46	28.5	3	0.68	1.91	1.10

SP818 / SP825 / SP842

	D_x (mm)					D_x (stand.)			
	N	M	SD	SE	V	N	M	SD	SE
A	-	-	-	-	-	5	0.34	1.05	0.47
B	-	-	-	-	-	32	0.06	0.97	0.17
C	-	-	-	-	-	6	-0.59	0.86	0.35

SP707

	D_x (mm)					D_x (stand.)			
	N	M	SD	SE	V	N	M	SD	SE
A	83	1.50	0.27	0.03	17.9	83	0.23	1.07	0.12
B	59	1.36	0.23	0.03	16.5	59	-0.29	0.90	0.12
C	16	1.40	0.18	0.04	12.6	16	-0.14	0.70	0.18

JT7911

	D_x (mm)					D_x (stand.)			
	N	M	SD	SE	V	N	M	SD	SE
A	9	1.45	0.45	0.15	30.8	9	0.50	1.58	0.53
B	21	1.30	0.28	0.06	21.4	21	-0.03	0.99	0.22
C	29	1.27	0.21	0.04	16.7	29	-0.13	0.75	0.14

ALL DATA

	D_x (mm)					D_x (stand.)			
	N	M	SD	SE	V	N	M	SD	SE
A	-	-	-	-	-	111	0.22	1.06	0.10
B	-	-	-	-	-	131	-0.13	0.96	0.08
C	-	-	-	-	-	54	-0.14	0.84	0.11

TABLE XVIII: Real and standardized mean D_X values and associated statistics of the three morphogroups in four European (lump-)samples and in all these samples together.

IR496

		D_X (mm)				D_X (stand.)			
	N	M	SD	SE	V	N	M	SD	SE
A	23	1.98	0.28	0.06	14.3	23	-0.10	1.01	0.21
B	47	1.99	0.24	0.04	12.1	47	-0.06	0.86	0.13
C	30	2.06	0.34	0.06	16.4	30	0.17	1.20	0.22

IR470

		D_X (mm)				D_X (stand.)			
	N	M	SD	SE	V	N	M	SD	SE
A	1	-	-	-	-	1	-	-	-
B	32	2.07	0.29	0.05	14.2	32	0.12	1.03	0.18
C	15	1.98	0.27	0.07	13.7	15	-0.21	0.95	0.24

ALL DATA

		D_X (mm)				D_X (stand.)			
	N	M	SD	SE	V	N	M	SD	SE
A	24	1.97	0.28	0.06	14.1	24	-0.15	0.99	0.20
B	79	2.02	0.27	0.03	13.1	79	0.02	0.94	0.11
C	45	2.03	0.32	0.05	15.5	45	0.05	1.12	0.17

TABLE XIX: Real and standardized mean D_X values and associated statistics of the three morphogroups in samples IR469 and IR470 and in both samples together.

		O_i (mm)		E_i (%)		A_i (mm^2)		k_i	
i	N	M	SE	M	SE	M	SE	M	SE
3	70	0.986	0.017	29.5	0.6	0.074	0.003	-	-
4	70	1.134	0.021	36.3	0.9	0.097	0.004	1.321	0.013
5	70	1.307	0.026	38.8	0.7	0.129	0.005	1.324	0.008
6	70	1.508	0.030	39.0	0.8	0.172	0.007	1.331	0.010
7	70	1.701	0.036	37.3	1.0	0.221	0.009	1.280	0.010
8	70	1.917	0.042	40.4	1.0	0.282	0.012	1.277	0.008
9	70	2.157	0.047	42.7	0.9	0.358	0.016	1.266	0.007
10	70	2.402	0.053	43.9	1.1	0.447	0.020	1.248	0.007
11	70	2.684	0.061	48.8	1.0	0.562	0.025	1.257	0.008
12	70	2.971	0.066	50.1	1.3	0.689	0.031	1.229	0.008
13	70	3.288	0.072	55.1	1.2	0.848	0.037	1.234	0.007
14	70	3.647	0.081	59.7	1.3	1.048	0.047	1.237	0.007
15	70	4.040	0.091	65.0	1.6	1.291	0.058	1.231	0.006
16	69	4.438.	0.097	69.9	1.6	1.554	0.067	1.227	0.007
17	68	4.888	0.105	74.4	2.0	1.877	0.080	1.223	0.008

TABLE XX: Mean values and standard errors of parameters O_i, A_i, E_i (i = 3 - 17) and k_i (i = 4 - 17) of *C. mediterraneus* in Ramla.

i	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
N	70	70	70	70	70	70	70	70	70	70	70	70	70	69	68
	r	r	r	r	r	r	r	r	r	r	r	r	r	r	r
O_i - c_{12}	**0.93**	**0.89**	**0.87**	**0.85**	**0.85**	**0.80**	**0.80**	**0.78**	**0.76**	**0.76**	**0.74**	**0.71**	**0.69**	**0.67**	**0.64**
O_i - X	**-0.54**	**-0.59**	**-0.62**	**-0.65**	**-0.66**	**-0.66**	**-0.68**	**-0.70**	**-0.70**	**0.72**	**-0.75**	**-0.74**	**-0.77**	**-0.77**	**-0.77**
O_i - γ	**-0.71**	**-0.73**	**-0.73**	**-0.76**	**-0.76**	**-0.75**	**-0.76**	**-0.76**	**-0.75**	**-0.76**	**-0.76**	**-0.74**	**-0.74**	**-0.74**	**-0.74**
O_i - D_X	-0.05	-0.07	-0.05	-0.05	0.00	0.02	0.01	0.03	0.02	0.00	-0.01	0.03	0.01	0.06	0.09
O_i - E_i	0.10	**0.40**	**0.52**	**0.46**	**0.62**	**0.64**	**0.58**	**0.62**	**0.73**	**0.62**	**0.75**	**0.81**	**0.84**	**0.80**	**0.74**
O_i - k_i	-	*0.26*	**0.35**	0.17	**0.38**	*0.25*	0.19	0.10	0.15	0.00	-0.04	0.05	0.15	-0.00	0.01
O_i - $\bar{k}$	-0.19	-0.09	0.00	0.08	0.14	0.20	*0.23*	*0.27*	**0.30**	**0.35**	**0.40**	**0.44**	**0.49**	**0.49**	**0.52**
E_i - c_{12}	0.02	*0.23*	**0.41**	**0.32**	**0.39**	**0.34**	**0.39**	**0.35**	**0.52**	**0.43**	**0.49**	**0.52**	**0.52**	**0.58**	**0.37**
E_i - X	*-0.27*	*-0.27*	**-0.32**	**-0.37**	**-0.38**	**-0.46**	**-0.54**	**-0.51**	**-0.72**	**-0.57**	**-0.73**	**-0.77**	**-0.87**	**-0.84**	**-0.80**
E_i - γ	**-0.30**	**-0.30**	**-0.42**	**-0.40**	**-0.44**	**-0.47**	**-0.53**	**-0.48**	**-0.68**	**-0.50**	**-0.62**	**-0.70**	**-0.74**	**-0.75**	**-0.67**
E_i - D_X	-0.02	0.05	0.15	0.00	0.12	0.05	-0.13	-0.09	*-0.28*	-0.20	-0.20	-0.16	**-0.30**	**-0.30**	*-0.29*
E_i - k_i	-	**0.66**	**0.55**	**0.69**	**0.83**	**0.67**	**0.51**	**0.64**	**0.42**	**0.59**	**0.38**	**0.31**	**0.40**	0.20	**0.39**
E_i - $\bar{k}$	*0.29*	0.20	*0.26*	*0.27*	**0.30**	**0.37**	**0.35**	**0.33**	**0.39**	**0.36**	**0.48**	**0.55**	**0.53**	**0.45**	**0.56**
k_i - c_{12}	-	-0.02	0.13	-0.01	0.18	-0.14	0.05	-0.08	-0.09	-0.07	**-0.32**	-0.21	-0.10	-0.16	-0.18
k_i - X	-	*-0.27*	**-0.34**	**-0.32**	*-0.23*	-0.12	*-0.25*	-0.11	-0.14	-0.15	-0.04	0.01	**-0.30**	-0.10	-0.14
k_i - γ	-	-0.17	*-0.27*	-0.21	*-0.23*	-0.04	-0.21	-0.02	0.02	-0.04	0.12	0.15	-0.11	0.03	-0.07
k_i - D_X	-	-0.10	0.09	0.02	0.23	0.17	-0.03	0.04	-0.07	-0.13	0.03	0.22	-0.14	-0.02	-0.17
k_i - $\bar{k}$	-	**0.39**	**0.47**	**0.61**	**0.34**	**0.38**	**0.33**	*0.25*	**0.33**	**0.29**	**0.34**	**0.39**	**0.42**	**0.34**	**0.31**

TABLE XXI: Correlation coefficients of parameter combinations involving O_i, A_i, E_i and/or k_i as calculated for successive ontogenetic stages of *C. mediterraneus* in Ramla. Significance levels
italics: $p < 0.05$
bold : $p < 0.01$

			O_i		E_i (%)		A_i (mm²)		k_i											
		N	M	SE	M	SE	M	SE	M	SE										
	A	13	0.964	0.050	29.3	1.4	0.072	0.007	-	-		A	13	2.379	0.148	43.5	2.2	0.444	0.053	1.249	0.016
3	B	36	1.018	0.021	30.0	0.7	0.078	0.003	-	-	10	B	36	2.505	0.066	44.8	1.8	0.483	0.027	1.245	0.011
	C	21	0.946	0.032	28.7	1.2	0.068	0.004	-	-		C	21	2.239	0.093	42.7	1.6	0.386	0.032	1.251	0.013
	A	13	1.126	0.065	38.4	1.6	0.098	0.011	1.342	0.028		A	13	2.674	0.158	48.5	1.9	0.560	0.063	1.277	0.019
4	B	36	1.175	0.025	36.4	1.2	0.103	0.004	1.330	0.017	11	B	36	2.805	0.078	50.0	1.4	0.611	0.035	1.261	0.009
	C	21	1.070	0.037	34.9	1.8	0.087	0.006	1.292	0.025		C	21	2.483	0.107	46.9	2.1	0.479	0.040	1.238	0.017
	A	13	1.299	0.078	39.9	2.0	0.130	0.015	1.323	0.019		A	13	2.946	0.172	48.5	2.8	0.683	0.075	1.222	0.024
5	B	36	1.353	0.030	39.2	0.8	0.137	0.006	1.332	0.012	12	B	36	3.105	0.086	51.7	1.8	0.747	0.043	1.224	0.010
	C	21	1.232	0.046	37.7	1.6	0.115	0.008	1.311	0.014		C	21	2.756	0.114	48.3	2.7	0.593	0.048	1.243	0.015
	A	13	1.499	0.090	39.6	2.2	0.172	0.019	1.333	0.024		A	13	3.226	0.176	51.7	2.8	0.819	0.084	1.212	0.019
6	B	36	1.565	0.036	39.2	1.2	0.183	0.008	1.338	0.015	13	B	36	3.444	0.097	56.8	1.7	0.924	0.054	1.237	0.009
	C	21	1.417	0.055	38.5	1.4	0.152	0.011	1.319	0.016		C	21	3.058	0.125	54.1	1.8	0.735	0.059	1.241	0.012
	A	13	1.701	0.105	36.0	2.1	0.223	0.026	1.286	0.020		A	13	3.566	0.193	58.0	2.1	1.006	0.102	1.238	0.019
7	B	36	1.764	0.043	38.2	1.2	0.235	0.011	1.280	0.014	14	B	36	3.828	0.108	62.1	1.8	1.147	0.067	1.242	0.008
	C	21	1.592	0.064	36.4	2.1	0.194	0.015	1.274	0.019		C	21	3.388	0.143	56.4	2.9	0.905	0.077	1.227	0.014
	A	13	1.906	0.124	39.8	2.4	0.283	0.035	1.263	0.016		A	13	3.923	0.212	62.6	3.7	1.222	0.123	1.216	0.015
8	B	36	1.988	0.049	41.7	1.2	0.301	0.015	1.279	0.009	15	B	36	4.257	0.122	67.8	2.2	1.425	0.085	1.241	0.009
	C	21	1.803	0.076	38.6	2.0	0.250	0.021	1.282	0.021		C	21	3.740	0.159	61.7	2.8	1.105	0.092	1.223	0.012
	A	13	2.141	0.136	43.9	2.3	0.357	0.043	1.264	0.016		A	13	4.302	0.233	67.0	3.5	1.469	0.150	1.203	0.015
9	B	36	2.250	0.057	43.8	1.1	0.386	0.020	1.282	0.010	16	B	35	4.670	0.124	72.7	2.1	1.710	0.095	1.238	0.011
	C	21	2.008	0.085	40.1	1.8	0.311	0.027	1.241	0.012		C	21	4.134	0.176	67.1	2.9	1.348	0.110	1.223	0.011
												A	13	4.696	0.247	70.2	5.0	1.736	0.171	1.188	0.022
											17	B	34	5.147	0.136	77.1	2.6	2.066	0.114	1.229	0.011
												C	21	4.588	0.190	72.6	3.7	1.659	0.131	1.236	0.013

TABLE XXII: Mean values and standard errors of parameters O_i, A_i, E_i and k_i in the early ontogenetic stages of the three morphogroups in *C. mediterraneus* from Ramla.

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